

Fossil plants from the Upper Permian in the Mooi River district of Natal, South Africa

by

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SYNOPSIS

A flora of 35 taxa is described from the *Daptocephalus* reptile zone of the Lower Beaufort Subgroup in Natal. It is associated with a rich insect fauna. The flora consists mainly of sphenopsids (four species), pteropsids (one species), cycadopsids, chiefly *Glossopterideae* (fifteen species), coniferopsids (one species), dispersed seeds and microsporangia.

Three new monotypic genera of fructifications, probably all *glossopteridean*, are erected: *Mooia* (*lidgettonioides*), *Rusangea* (*elegans*), *Rigbya* (*arberioides*).

Two new fructifications are placed in existing *glossopteridean* fructification genera: *Scutum conspicuum* attached to leaves of *Glossopteris conspicua* Feistmantel, and *Plumsteadia natalensis* attached to narrow leaves resembling *Glossopteris indica* Schimper.

One new species is placed in an existing, probably *glossopteridean*, leaf genus: *Belemnopteris elongata*.

One new monotypic genus is erected for a problematic plant which may be a moss: *Buthelezia (mooiensis)*.

The flora shows affinity with those of the Raniganj Stage (Upper Damuda Series) of India, the Newcastle and Upper Bowen Series of Australia, and the Ohio Range of Antarctica.

CONTENTS

| | Page |
|---|------|
| Introduction | 349 |
| Earlier work on Upper Permian plants in Natal | 350 |
| Locality and Horizon | 352 |
| Material and Methods | 353 |
| Systematic description of the fossil flora of the Mooi River site | 354 |
| Sphenopsida — Equisetales | 354 |
| — Sphenophyllales | 357 |
| Pteropsida — Filicales | 357 |
| Cycadopsida — Pteridospermales—Glossopterideae | 360 |
| — Sterile leaves and scales | 360 |
| — Fructifications and seeds | 378 |
| Coniferopsida — Cordaitales or Coniferales | 407 |
| Incertae Sedis | 409 |
| Discussion | 415 |
| Composition of the Mooi River Flora | 415 |
| Botanical considerations | 416 |
| Geological considerations | 417 |
| Acknowledgements | 418 |
| References | 418 |

INTRODUCTION

This paper presents the main results of a study of a large new collection of fossil plants from the Upper Permian of Natal. The collection is of exceptional interest. It contains a wealth of vegetative and reproductive material which adds considerably to the knowledge of the flora of this time and many of the taxa strengthen correlations between South Africa and other parts of Gondwanaland, notably India, Australia and Antarctica.

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Earlier work on Upper Permian plants in Natal

There have been comparatively few previous studies. One of the earliest is that of Etheridge (1902), who recorded the following taxa from the St Lucia (Somkele) Coalfield:

Phyllothea zeilleri Etheridge
Glossopteris browniana Brongniart var. *indica* Bunbury
G. browniana Brongniart var. *angustifolia* Brongniart
G. damudica var. *stenoneura* Feistmantel
G. retifera Feistmantel
Angiopteridium spathulatum McClelland

A few years later Seward (1908) also recorded a collection of plants from the St Lucia area:

(a) from the Somkele district

Phyllothea zeilleri Etheridge
Glossopteris indica Schimper
G. browniana Brongniart
G. retifera Feistmantel
Vertebraria indica Royle

(b) from the Umlalaas district

Phyllothea zeilleri Etheridge
Glossopteris browniana Brongniart
Vertebraria indica Royle

In the same paper Seward (1908) recorded *Noeggerathiopsis hislopii* (Bunbury) Feistmantel from Ramsay Colliery, near Newcastle.

Nearly a quarter century later an important paper by Du Toit (1932a) added the following taxa from a locality north-west of Bergville at an horizon near the top of the Lower Beaufort Beds:

Phyllothea australis Brongniart
Schizoneura gondwanensis Feistmantel
Sphenophyllum speciosum (Royle) McClelland
Sphenopteris alata (Brongniart) Brongniart
Glossopteris indica Schimper
G. browniana Brongniart
G. retifera Feistmantel
Eretmonia natalensis Du Toit (as new taxon)

In the same paper Du Toit (1932a) recorded the following taxa from localities near Inhluzani Mountain, Nottingham Road district, at an horizon in the lower part of the Lower Beaufort:

Glossopteris cordata Feistmantel *non* Dana
G. retifera Feistmantel
G. conspicua Feistmantel

From Glencalder, near Newcastle, Du Toit (1932a) also recorded *Glossopteris retifera* Feistmantel.

Some twenty years later Du Toit (1954) published a revised list of Upper Permian (Lower Beaufort) fossil plants. This included all the earlier Natal records, except that Etheridge's *Glossopteris damudica* var. *stenoneura* Feistmantel was omitted and

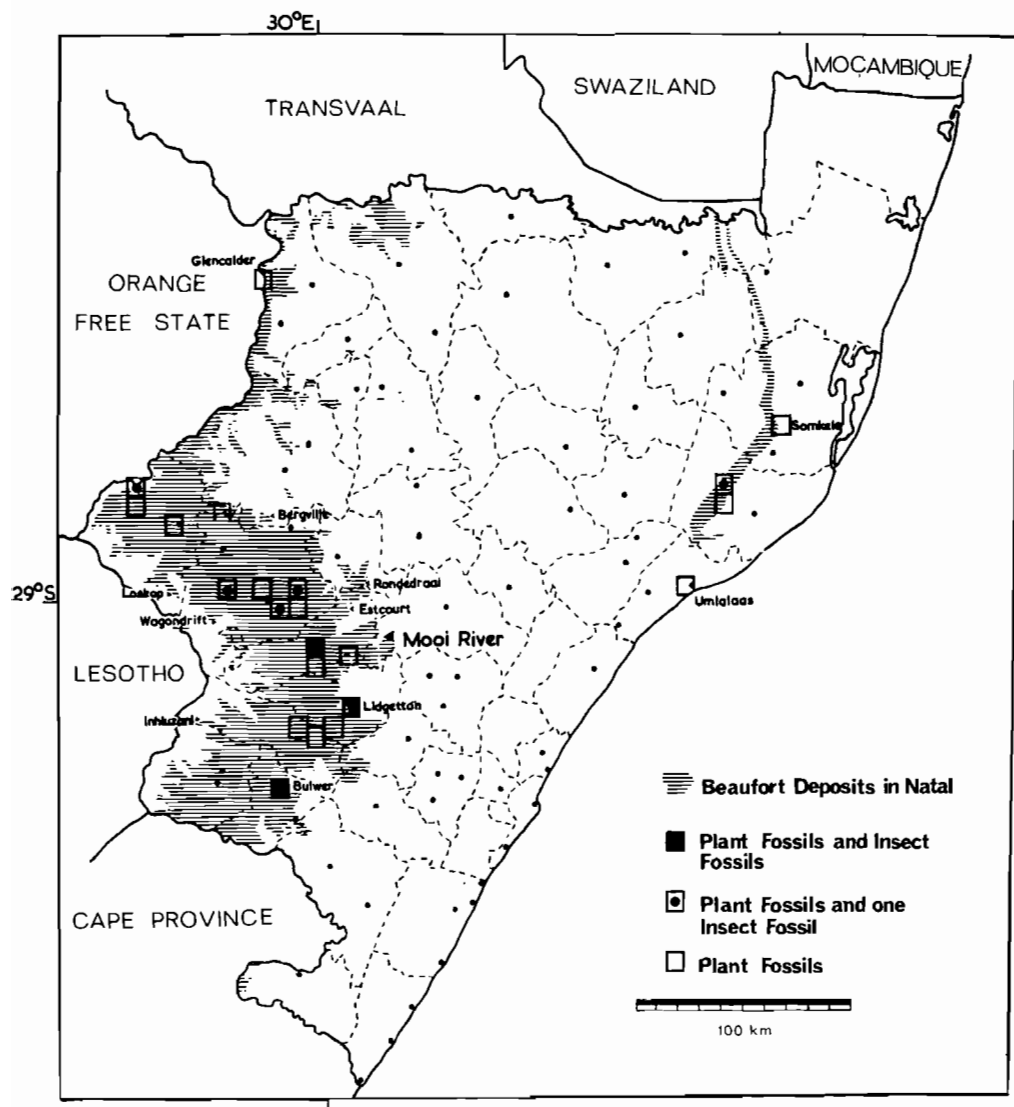


Fig. 1. Beaufort Plant Fossil Localities in Natal. Published and unpublished localities from various sources; localities which have been mentioned in publications are named. To the west of the main Beaufort deposits are younger deposits (Stormberg), and to the east older deposits (Ecca, Dwyka and Pre-Karoo); the Beaufort deposits in the east lie eastward of the Natal Monocline and are margined to the east by younger deposits (Stormberg and Cretaceous); the limits of the Ecca and the eastern Beaufort are largely inaccurately known and the localities in this region are also rather imprecisely defined at present. The mapping of the Beaufort follows the 1 : 1 000 000 Geological Map of the Republic of South Africa 1970.

replaced by *G. ampla* Dana and *Angiopteridium spathulatum* appeared as *Taeniopteris* (*Angiopteridium*) *spathulata* (McClelland). Du Toit (1954) also added *G. ampla* Dana from Inhluzani and *G. indica* Schimper from Estcourt.

From Lidgetton, near Pietermaritzburg, Thomas (1958) cited the following taxa:

cf. *Neocalamites carreri* Zeiller

Glossopteris cf. *indica* Schimper, *communis* Feistmantel and *arberi* Srivastava

Lidgettonia africana Thomas (as new taxon)

Samaropsis cf. *S. seixasi* (White) Sew.

microsporangia (now known as *Arberiella* Pant & Nautiyal)

Two recent taxonomic papers necessitate changes in some of the specific names given above. Rigby (1964) has proposed the new name *Glossopteris feistmantelii* for *G. cordata* Feistmantel non Dana listed by Du Toit (1932a); Schopf, Maheshwari & Rigby (in press) suggest *Glossopteris elongata* Dana in place of *G. retifera* Feistmantel (which is a junior synonym). Plumstead (1972) recorded *Phyllothea etheridgei* Arber and *Dictyopteridium sporiferum* Feistmantel from a borehole sunk at Somkele in 1964–1966.

The most recent reference to the Upper Permian Flora of Natal is a preliminary communication by Lacey, Van Dijk & Gordon-Gray (1974) on the material which forms the subject of the present paper.

Locality and Horizon

During construction work on the national throughway some 80 km north-west of Pietermaritzburg cuttings on the Mooi River–Estcourt by-pass exposed richly fossiliferous shales of Lower Beaufort age (see fig. 1). The most productive outcrops were subsequently destroyed as the roadworks proceeded, but fortunately one of us (D. E. van Dijk) was able to organize the collection of a large amount of material from the temporary exposures soon after their discovery.

The beds contain numerous insect remains as well as abundant plants. They are thought to lie in the *Daptocephalus* Zone (Kitching 1972) in the upper part of the Lower Subgroup of the Beaufort Group, Karroo Supergroup. This is of Upper Permian age, also suggested by the associated insect fauna which was referred to Dr E. F. Riek, C.S.I.R.O., Australia for study (Riek 1973, 1974).

The roadworks in the Mooi River–Estcourt locality also resulted in the opening of a small quarry for ballast, adjacent to the site. This lies stratigraphically slightly above the fossiliferous beds which are no longer exposed, but falls within the same subdivision of the Beaufort. The quarry yielded a fossil flora which is essentially similar to that from the lower horizon, but it differs in respect of the sizes attained by many of the plants and also contains several additional taxa, including slender, possibly coniferalean, leafy twigs and *Dictyopteridium* sp. This flora is also being studied and will be the subject of a later report.

An excavation, financed by the University of Natal and under permit from the National Monuments Council, which links the quarry with the road lying on the original site, has recently been completed. At the base of this excavation are dark shales from which microscopic plant remains have already been obtained. These shales may prove suitable for continued further study (see Material and Methods, no. 5, p. 354).

Material and Methods

Development of the bulk material collected in the field has resulted in the production of more than 1 000 selected hand-specimens. In addition, numerous large representative slabs are held in reserve. The collection is housed in the Natal Museum, Pietermaritzburg, registered under the numbers NM 1001 to NM 2500.

The plant fossils are preserved in a well-bedded, thinly laminated, very fine-grained shale. In most cases the colour of the shale varies from cream through buff and light reddish-brown to light grey. All such material is fairly soft and can be easily worked with dissecting instruments or trimmed to shape with a hack-saw or band-saw. Occasional bands of shale are dark grey in colour and harder.

The plants occur as impressions and incrustations in the fine-grained matrix (Lacey 1963). In the paler-coloured shales the original plant material is almost completely oxidized and the fossils appear as reddish-brown impressions. In many cases a thin layer of carbon still covers the impressions. Both this residual carbonaceous material and the underlying impressions in the fine rock matrix frequently show the cellular pattern of the epidermis very clearly. The harder, dark-coloured shales contain less-oxidized plant material; indeed, sufficient thickness of carbonaceous substance remains to consider them as incrustations.

Since no organic matter remains in most of the specimens, examination by reflected light has been employed. Most specimens have been studied under a binocular microscope with strong low-angle unilateral illumination from a Tiyoda 8,8 V 5A focusing bench light. A few specimens have been improved by immersion in xylol or very briefly in water.

Repeated attempts to make maceration and transfer preparations (Lacey 1963) from plants preserved as incrustations in the harder, darker-coloured shales have met with varying degrees of success. The results are summarized:

1. Carbonaceous fragments of leaves of *Noeggerathiopsis hislopii*, *Sphenophyllum speciosum* and *Sphenopteris alata*, all showing good cellular pattern both in the carbon and in the underlying matrix, were subjected to maceration for 24 hours in Schultze solution, followed by washing in water, and the addition of a few drops of very dilute ammonia solution. They dissolved completely, indicating that only carbon is present, and that no cuticles (or perhaps only exceedingly thin cuticles) are preserved.

2. Similar results were obtained when four samples of *Glossopteris* leaves preserved as carbonaceous incrustations on harder grey shales were similarly treated with Schultze solution followed by dilute alkali. However, fragments macerated in Schultze solution, *without* subsequent treatment in alkali, when mounted in polyvinyl lactophenol cleared and partially dissolved and showed a rather obscure cellular pattern. This pattern took the form of elongated cells following the original course of the veins, with isodiametric cells and regular cavities in the areolae between the veins.

The conclusion was drawn that in such incrustations the original substance of the leaf mesophyll is preserved largely as carbon, but that no cuticle is preserved, or that a very thin cuticle is present on the carbonaceous fragments or left adhering to the rock matrix.

3. Attempts were therefore made to prepare cuticles from further samples of carbonaceous *Glossopteris* leaves on grey shales by cellulose acetate pull technique, but these

yielded little of value. The acetate pulls showed an impression of a cellular pattern, but this was no more informative than an examination of the original fossil surface or impression in the matrix by reflected light.

4. A similar attempt to prepare Walton transfers, using Lakeside 70 resin, from carbonaceous fragments of *Sphenophyllum speciosum* was also unsuccessful, but a transfer of *Sphenopteris alata*, using thick cellulose acetate butyrate sheet, yielded a mesophyll pattern of veins and intervening assimilatory cells.

5. Bulk maceration of hard dark-grey shales lacking identifiable macro-fossils, using hydrofluoric acid followed by oxidative maceration in Schultze solution and mounting in polyvinyl lactophenol, yielded fairly well-preserved bisaccate pollen grains and fragments of leaf epidermis cuticle.

This latter result indicates that the potentialities exist for the preparation of cuticles by maceration and for palynological work if suitable unoxidized shales can be located in the Mooi River area. Available material from the recent excavation at the site (see above) is being further studied.

SYSTEMATIC DESCRIPTION OF THE FOSSIL FLORA OF THE MOOI RIVER SITE*

SPHENOPSIDA

EQUISETALES

Impressions of detached equisetaceous leaf-sheaths occur occasionally. Three types are present. They may be parts of the same plant, but this cannot be proved and for the present they are treated separately.

Genus *Phyllothea* Brongniart, 1828

Phyllothea australis Brongniart

Specimen figured NM 1868b

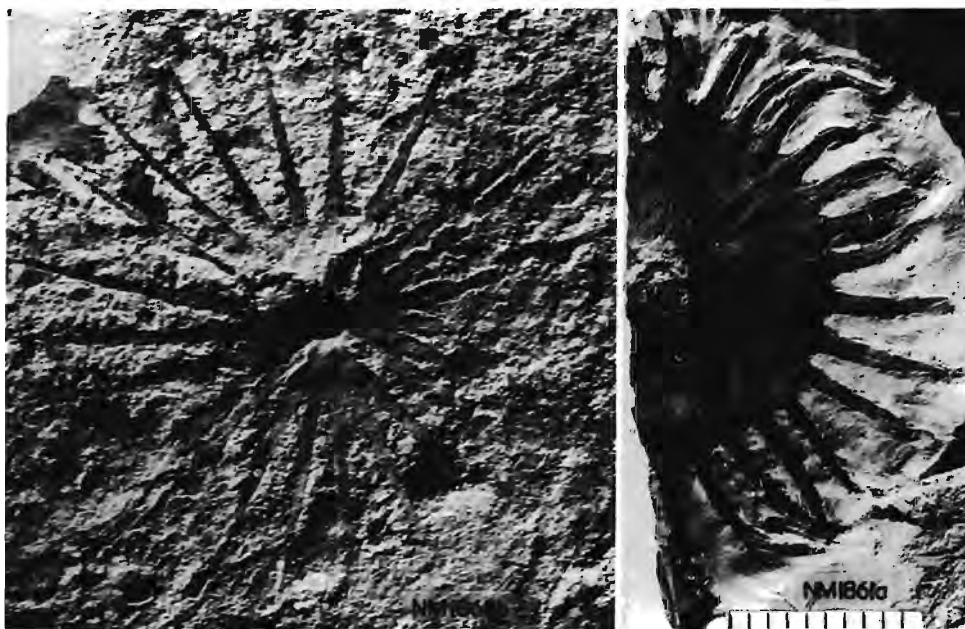
Six specimens are included in this widespread Gondwana species. They possess a somewhat funnel-shaped sheath opening into a disc, 4 to 9 mm in diameter, from which the free parts of 14 to 22 leaves arise, the whorls having a total width from leaf tip to leaf tip of 28 to 32 mm. In their free parts the individual leaves are slender, with a single broad median vein which, however, is not easily seen. At the point where they become free from the disc the leaves are about 1 mm wide and they taper gradually to a fine point. They appear to be adaxially channelled, with a slightly revolute narrow margin. In the disc the fusion of the individual leaves is marked by a fine line.

Phyllothea cf. etheridgei Arber

Specimen figured NM 1861a

Three specimens of leaf-sheaths differ in several respects from *Phyllothea australis* described above. They show greater fusion of the leaves, producing a disc 12 to 19 mm

* *Note:* In citing the specimens photographed to illustrate this section, the following procedure has been adopted: 1. Where there is more than a single specimen, the sequence of numbers follows that of the composite figure from left to right, top to bottom. 2. Where a number is followed by letters of the alphabet: (i) 'a and b' indicates part and counterpart are included in the same photograph; (ii) 'a, b' indicates part and counterpart are shown in two photographs; (iii) 'b, a' indicates the counterpart is given first; (iv) two numbers separated by; indicates the two photographs are included in successive composite figures.



NM 1868b: *Phyllothea australis* Brongniart $\times 2,5$ (left). NM 1861a: *Phyllothea* cf. *etheridgei* Arber $\times 2,5$ (right).

in diameter, from which 28 to 32 free parts of leaves arise, the whorls having a total width of 26 to 36 mm. In effect, the leaf whorls are larger overall, with more leaves and a much greater degree of fusion.

Such specimens show marked resemblance to the middle region of specimens of *Phyllothea etheridgei* Arber as reconstructed by Saksena (1954). In detail, however, the individual leaves have a similarity to *P. australis* Brongniart, having a strong single vein, canaliculate upper surface and revolute margin. Rigby (1974, pers. comm.) states that the leaves in *P. australis* can be almost completely fused, so it may be that the specimens described here should be referred to that species.

Indeed, if Rigby (pers. comm.) is correct in assigning *Phyllothea etheridgei* to *Raniganjia bengalensis* (Feistmantel) Rigby on the basis of mucronate tips to the leaves, the only course of action open would be for these three Mooi River specimens to be included in *Phyllothea australis*.

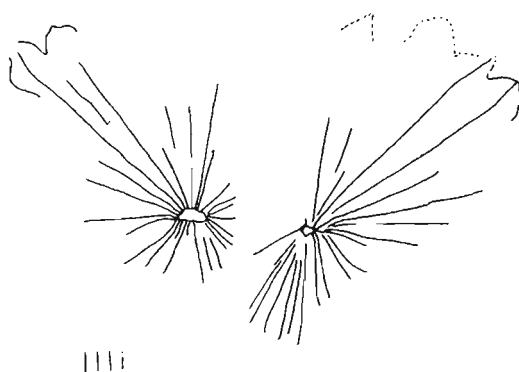
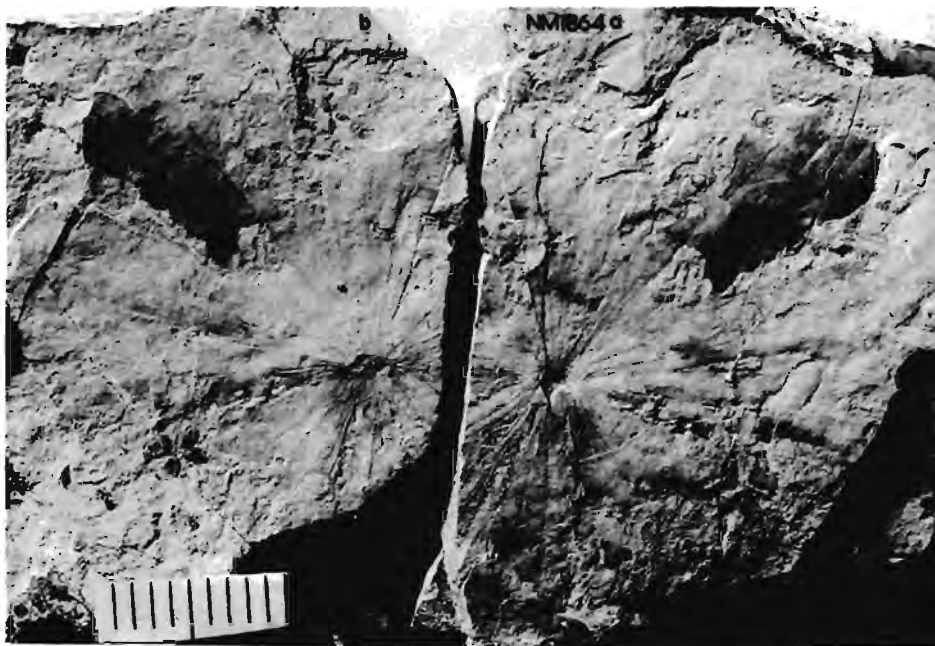
Genus *Raniganjia* Rigby, 1963

cf. *Raniganjia bengalensis* (Feistmantel) Rigby

Specimen figured NM 1864

Four specimens of leaf whorls show almost complete fusion of the leaves into a flattened disc with crenate margin. The sheathing central part is scarcely developed. The whorls range from 26 to 42 mm in overall diameter, with a disc 22–24 to 38–40 mm (i.e. to the bottom of the sinus between teeth). The number of leaves forming the disc ranges from 25 to 32 and individual leaves are about 3,5 mm wide at the distal end just below the apex.

Each leaf has a single strong median vein which reaches the apex almost undiminished and may be emergent. There is a faint suggestion of striations in the leaf lamina at right angles to the midrib. The leaves appear to have been of a different texture (thinner or perhaps fleshy?) compared with those of *Phyllothea australis*. They have much in common with *Raniganjia bengalensis*, but the failure to recognize mucronate tips in the Natal specimens, which Rigby (1974, pers. comm.) regards as a feature distinguishing *Raniganjia* from *Phyllothea* and *Stellothea*, makes it



NM 1864b and a: *Raniganjia bengalensis* (Feistmantel) Rigby $\times 2.5$.

BELOW: Line tracing showing one leaf apex and the course of mid-veins and lines of leaf fusion in a single leaf whorl (NM 1864b and a).

impossible to identify them with certainty. Rigby (1963 and 1974, pers. comm.) now includes *Actinopteris bengalensis* Feistmantel, 1876, *Phyllothea etheridgei* Arber, 1905a, *Actinopteris indica* Srivastava, 1955, *Umbellaphyllites ivini* and *U. minima* Rigby, 1966, 1970, all in *Raniganjia bengalensis* (Feist.) Rigby.

SPHENOPHYLLALES

Genus *Sphenophyllum* Brongniart, 1822

Sphenophyllum speciosum (Royle) McClelland

Syn. *Trizygia speciosa* Royle

Specimens figured NM 1848, NM 1837

This well-known Lower Gondwana species is represented by 22 specimens. Most of them consist of detached whorls of six leaves, each whorl showing the three pairs of leaves of different sizes characteristic of the species. Four specimens show two or more such whorls attached to a slender striated stem. The largest leaves are 1,7 cm long and 0,7 cm wide, being appreciably larger than in specimens of the same species from the Lower Beaufort at Bergville, Natal, previously described by Du Toit (1932a), but markedly smaller than in specimens known from the Ecca of Rhodesia (Lacey & Huard-Moine 1966).

Many of the leaves show the open dichotomous venation clearly, but it is nevertheless difficult to decide whether the veins enter the leaf as one strand or as two close together. In a few cases the leaves show a cellular pattern, but cuticles could not be prepared. The epidermal pattern of this species has already been illustrated by Pant & Mehra (1963) and Surange (1966b).

The Chinese species, *Sphenophyllum sino-coreanum* Yabe, is very similar to *S. speciosum* and may be conspecific with it (Halle 1927; Lacey & Huard-Moine 1966).

PTEROPSIDA

FILICALES

Genus *Sphenopteris* (Brongniart, 1822) Sternberg, 1825

Sphenopteris alata (Brongniart) Brongniart

Specimens figured NM 1802b, NM 2003

Fragments of sphenopterid foliage are fairly common. Some 30 specimens have been found, including apical and middle parts of fronds, but neither basal parts nor petioles are present.

By matching up pinnae of similar size in selected specimens it is estimated that the complete frond was at least 15 cm long. All the specimens show the markedly winged rachis characteristic of the species *Sphenopteris alata*. In this respect and in the details of the pinnae and pinnules they agree well with the description of this species given by Du Toit (1932a).

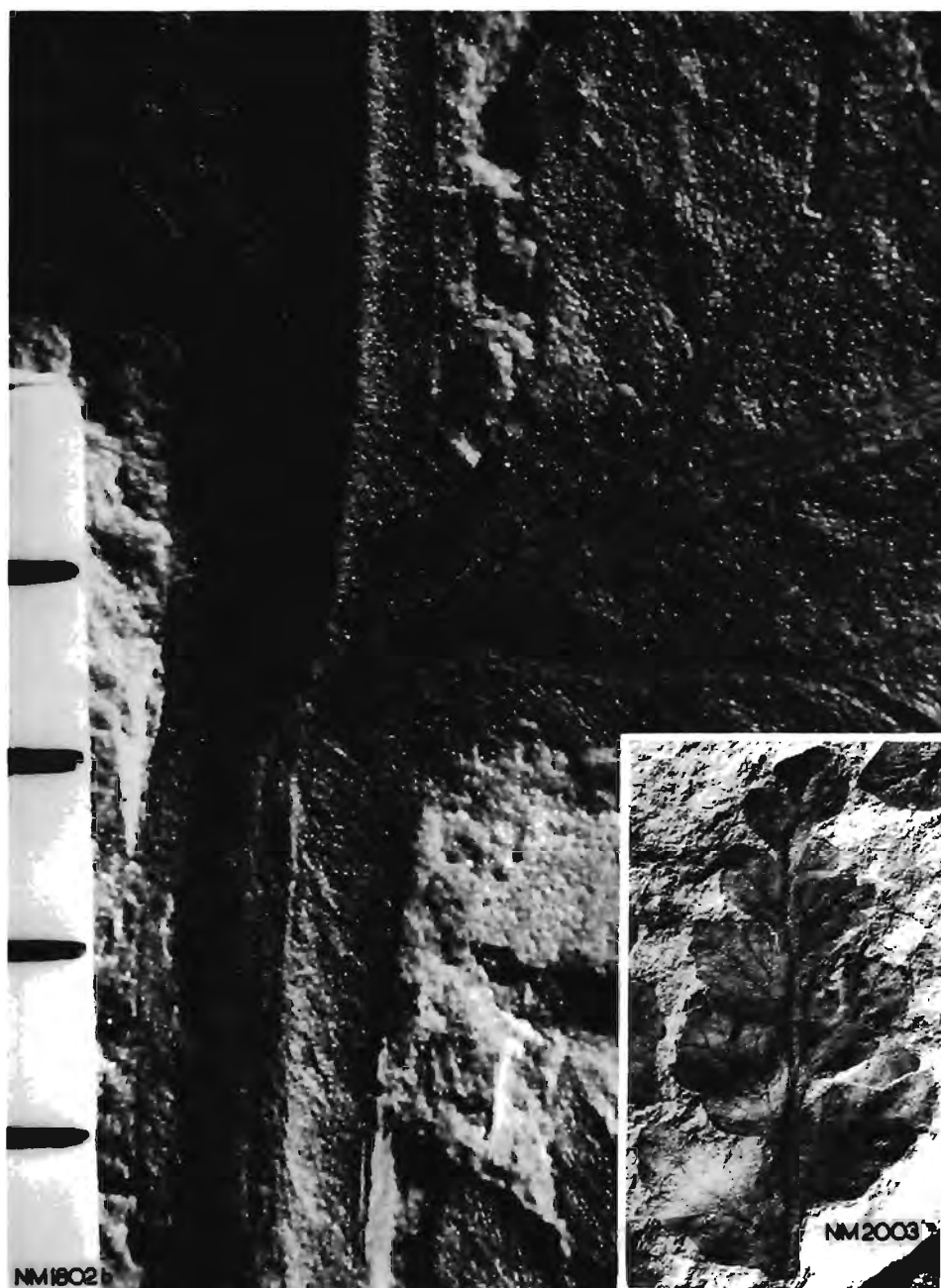
Several specimens show a distinct cellular pattern in the laminae of the pinnules, both as impressions in the matrix and also in the carbonaceous substance which occasionally remains (NM 1802b). Attempts to prepare cuticles from the latter were unsuccessful.

The filiclean nature of several Gondwana species of *Sphenopteris* has been confirmed by the discovery of fertile specimens (Lacey & Huard-Moine 1966; Rigby



NM 1848, 1837: *Sphenophyllum speciosum* (Royle) McClelland $\times 2,5$.

1972a). In *Sphenopteris alata*, Du Toit (1932a) states that *Dicksonia*-like sori occur on secondary veins in apical pinnae, but no detailed description or illustrations are provided. A search for fertile material in the present collection to confirm Du Toit's description met with no success. *Sphenopteris alata* must therefore be regarded as provisionally assigned to the Filicales at present.



NM 1802b, 2003: *Sphenopteris alata* (Brongniart) $\times 25$ and $\times 2.5$.

CYCADOPSIDA

PTERIDOSPERMALES

Glossopteridaceae

1. Sterile leaves and scales

Genus *Glossopteris* Brongniart, 1822

The leaf-genus *Glossopteris* was established by Brongniart for more or less lanceolate entire leaves possessing a midrib and finer secondary veins which form a reticulum by dichotomy and anastomosis. The first forms described came from India, Australia, Sweden and England. From its inception *Glossopteris* was a form or artificial genus.

In the latter part of the nineteenth century other workers, notably Feistmantel (1876, 1880, 1882, 1886) and Zeiller (1896, 1902), described many more forms from India, Australia, South Africa and South America. Nearly all of their species were founded on rather variable, and therefore unreliable, macroscopic features of leaf shape, size and vein pattern. Arber (1905a) made a brave attempt to classify the large number of forms then known, based largely on the nature of the secondary venation. He defined the genus in a more precise way and reduced the number of 'species' by interpreting them broadly.

In more recent years numerous additional forms have been described from all parts of Gondwanaland, but particularly from South America (Archangelsky 1958) and Antarctica (Plumstead 1962). At the present time about 80 forms have been described (Banerjee & Ghosh 1972).

During the last twenty years further attempts to classify *Glossopteris* leaves have been based on epidermal characters (Srivastava 1956; Surange & Srivastava 1956; Banerjee, 1968) and on attached reproductive structures (Plumstead 1958; Mukerjee, Banerjee & Sen 1966; Banerjee 1968). Thus four different schemes of classification have been tried based on (1) gross morphology, (2) secondary vein pattern, (3) epidermal structure, and (4) types of fructification. Unfortunately, no close agreement exists between these schemes, partly because, as Maheshwari (1966) and Banerjee (1968) point out, in many instances epidermal structures or fructifications have been described for leaf species incorrectly identified on macroscopic features!

Both Surange (1966) and Banerjee (1968) suggest that external, epidermal and reproductive characters should be considered together to achieve a satisfactory taxonomic arrangement. This is, of course, desirable but somewhat idealistic since type-specimens of many of the earliest described leaves are preserved in such a way that information on their epidermal or reproductive features is not available. Furthermore, most recent collections contain innumerable detached sterile leaves, variable in shape, size and degree of maturity, preserved only as impressions or compressions lacking cellular detail. Such leaves can be classified only on macroscopic vegetative features and up to a point their identification to species may often be suspect.

For these reasons, the sterile leaves described in the present account have been interpreted in a broad sense in the manner adopted by Lambrecht, Lacey & Smith (1973).

On this basis the following taxa have been recognized in the Mooi River collection:

Glossopteris browniana Brongniart

Glossopteris indica Schimper

Glossopteris angustifolia Brongniart

Glossopteris cf. *leptoneura* Bunbury

Glossopteris feistmantelii Rigby

Glossopteris conspicua Feistmantel

Glossopteris cf. *ampla* Dana

Glossopteris elongata Dana (syn. *G. retifera* Feist.)

Brief notes are given on each of these forms, but the chief diagnostic features are shown collected together in table 1 to facilitate ease of comparison and identification.

1. *Glossopteris browniana* Brongniart

Specimens figured NM 1767, NM 1762

This is probably the most commonly recorded, widely distributed and variable species of *Glossopteris*. It is frequent in the Mooi River collection. The leaves attain a large size, are ovate-lanceolate, with rounded apex, distinct midrib and secondary veins forming oblong-polygonal meshes pursuing an oblique course to the margin.

2. *Glossopteris indica* Schimper

Specimens figured NM 1774, NM 1765b; NM 1771

This form was originally described as a variety of *G. browniana*, which it much resembles.

These leaves may again attain a large size, but are more distinctly lanceolate with acute apex, stout midrib, and secondary veins forming rather narrow meshes pursuing an oblique course to the margin. The Mooi River collection contains a large number of specimens in this category.

Certain specimens in the collection have their secondary veins pursuing a closely parallel oblique course, forming very narrow meshes. Such forms have sometimes been recorded as *Glossopteris communis* Feistmantel, but they are not separated from *G. indica* in the present account. One such specimen is figured (NM 1771).

Leaves of the *Glossopteris indica-communis* type are also of common occurrence throughout Gondwanaland.

3. *Glossopteris angustifolia* Brongniart

Specimen figured NM 2010

This name is here used for narrow linear leaves, 2 cm or less in width, with closely set rarely anastomosing secondary veins, forming narrow elongate meshes, ascending to the margin very obliquely. This form is common in the collection.

4. *Glossopteris* cf. *leptoneura* Bunbury

Specimen figured NM 1766

(see after *G. elongata* for comparison therewith)

The collection contains a few narrow leaves, similar in size and shape to *G. angustifolia*, but distinguished by the secondary veins producing wide meshes. They are referred doubtfully to *G. leptoneura*. Some examples merge into *Glossopteris elongata* Dana (see below) from which they are not readily separated.

5. *Glossopteris feistmantelii* Rigby

Syn. *Glossopteris cordata* Feistmantel non Dana in Du Toit (1932a)

Specimen figured NM 1749

This name is here used for specimens ovate-cordate to oblong in shape, with coarse

TABLE 1

Diagnostic characters of sterile leaves mentioned in the text.

| <i>Species</i> | <i>Overall Shape</i> | <i>Base</i> | <i>Apex</i> | <i>†Midrib</i> | <i>Secondary Vein Pattern</i> | <i>Form of Meshes (Areolae)</i> |
|--|--|-------------|-------------------|---|---|--|
| 1. <i>Glossopteris browniana</i> Brongniart | Spathulate to ovate-lanceolate, often large | Contracted | Rounded or obtuse | Strong, persistent, sometimes ending just below apex (evanescent) | Acute to midrib, arching outwards to meet margin at 45°–90° | Oblong-polygonal, about 5 times as long as broad, narrower towards the margin |
| 2. <i>G. indica</i> Schimper | Lanceolate to ovate-lanceolate, often very large | Petiolate | Acute | Strong, persistent to apex | Acute to midrib, arching or unarched, pursuing an oblique course to margin at 45°–90° | Short, nearly iso-diametric and irregular near midrib, then narrow and very elongate towards margin |
| 3. * <i>G. communis</i> Feistmantel | Lanceolate to ovate-lanceolate, often very large | Petiolate | Acute to rounded | Strong, persistent | Acute to midrib, arched then parallel to one another and equally spaced through lamina, to meet margin at 20°–45° | Very elongate-polygonal, few anastomoses (usually 1 to 4 from midrib to margin) |
| 4. <i>G. angustifolia</i> Brongniart | Narrow, linear, small, 1–2 cm broad | Petiolate | Acute | Distinct, persistent | Acute to midrib, pursuing a steeply oblique course, to meet margin at 15°–30° | Narrow, elongate-polygonal, few anastomoses (up to 3) from midrib to margin ('taeniopteroid' appearance) |
| 5. <i>G. cf. leptoneura</i> Bunbury | Narrow, linear, small, up to 2 cm broad | Petiolate | Acute | Distinct | Slightly oblique to midrib, arched, meeting margin at 30°–70° | Elongate-polygonal to widely polygonal, sometimes triangular near midrib, narrower towards margin |

| | | | | | | |
|--|--|---|---------------------------------------|--|---|--|
| 6. <i>G. feistmantelii</i> Rigby | Variable, reniform or ovate-cordate to oblong, fairly small | Petiolate | Broadly ovate to obtusely dointed | Strong, persistent | Oblique to midrib, arched, in upper part meeting margin at 60°–80°, in mid region at 90°, and in base reflexed | Coarse, very open, oblong polygonal (cf. <i>G. elongata</i> and <i>G. conspicua</i>) |
| 7. <i>G. conspicua</i> Feistmantel | Spathulate to ovate-lanceolate, fairly small, not usually over 7 cm long | Contracted, sometimes with shoulders (truncate) | Rounded | Distinct, but may be evanescent | Oblique to midrib, arched, about 2 mm apart, pursuing an acute course from midrib to margin | Coarse, open polygonal to elongate-hexagonal, sometimes becoming smaller towards the margin |
| 8. <i>G. cf. ampla</i> Dana | Broadly ovate, often large | Contracted | Broadly rounded, sometimes emarginate | Distinct, very wide at base, persistent | Acute, oblique, arched towards midrib, becoming straight and parallel towards margin, approached at 60°–90° | Elongate-polygonal, often much narrower and longer towards margin |
| 9. * <i>G. damudica</i> Feistmantel | Broadly ovate to ovate-lanceolate | Contracted | Obtuse, rounded | Distinct, broad | After curving rapidly from midrib, almost perpendicular throughout to margin, about 1 per mm towards midrib, 2 per mm at margin | Sub-triangular near midrib, then narrow-elongate, narrower and shorter near margin |
| 10. <i>G. elongata</i> Dana | Ovate-lanceolate or lanceolate, fairly small | Petiolate | Acute to rounded | Distinct | Slightly oblique and arched near midrib, then perpendicular throughout to margin | Coarse, wide, slightly elongate-hexagonal, becoming narrower and shorter towards margin |
| 11. <i>Belemnopteris</i> sp. nov. | Elongate to ovate-lanceolate, with sagittate base | Petiolate | Probably obtusely pointed | Strong, with a lateral branch to each basal lobe | Oblique and ascending in most of the lamina, then at 90° to the margin near the base and reflexed in the basal lobes | Coarse, open slightly elongate-hexagonal or polygonal, smaller near the margin (cf. <i>Glossopteris elongata</i>) |

* Not treated as separate species in this account.

† All the leaves described have a striated midrib.



NM 1767, 1762 and 1762 enlarged: *Glossopterts browniana* Brongniart $\times 1$ and $\times 5$.

reticulation (resembling that in *G. elongata* and *G. conspicua*—see below), and distinct petiole. The species has been recorded previously by Du Toit (1932a) from Inhluzani, near Nottingham Road, in Natal.

6. *Glossopteris conspicua* Feistmantel

Specimens figured NM 1276a, NM 1754b, a

This name is applied to small spatulate to oval-lanceolate leaves, with a contracted, sometime truncate base, strong midrib, and obliquely ascending secondary veins forming rather coarse large meshes.

Six specimens of this species have been found, one with a fructification attached (see later).

7. *Glossopteris* cf. *ampla* Dana

Specimens figured NM 1761, NM 1775b

Several very large, broadly ovate leaves that seem to merge into *Glossopteris damudica* Feistmantel, which has not been recognized as a separate species in the present account, are included in this species. The secondary veins of these leaves pursue a closely parallel course which, except close to the midrib, is nearly perpendicular to margin and midrib.

8. *Glossopteris elongata* Dana, 1849Syn. *G. retifera* Feist. See Schopf, Maheshwari & Rigby (in press)Specimens figured NM 1770, NM 1779; *G. cf. elongata* NM 1777, NM 1776

Several examples of small ovate-lanceolate leaves, with distinct midrib and secondary veins forming large wide meshes which are arranged nearly perpendicular to midrib and margin are included in this species.

The species has some stratigraphical value since it is not known to extend above the Lower Beaufort (Du Toit 1954). In this connection it may be noted that species of the genus *Gangamopteris* do not extend beyond the Eccu, so that the presence of *Glossopteris elongata* in the Mooi River beds, from which *Gangamopteris* species are absent, can be taken as a reliable indication of Lower Beaufort age.

Genus *Belemnopteris* (Feistmantel, 1876) **emend.**

Six sterile leaves in the collection differ considerably from typical *Glossopteris*. They are entire, petiolate leaves, characterized by (1) a sagittate base, (2) division of the midrib into three, with a reflexed branch to the tip of each basal lobe, and (3) secondary veins forming a coarse reticulum, rather similar to that in *Glossopteris elongata* Dana.

These features are considered sufficient to place the new leaves in Feistmantel's (1876) genus *Belemnopteris*. Etheridge (1904) has commented on the tri-partite main vascular structure, with a lateral branch supplying each basal lobe, as an important diagnostic feature of the genus. However, the Mooi River leaves differ from the Indian type-species, *B. wood-masoniana* Feistmantel, in being narrowly rather than broadly sagittate and their inclusion in *Belemnopteris* necessitates slight emendation of the generic diagnosis.

Emended generic diagnosis: Leaves entire, base sagittate, petiolate. Midrib strong, divided into three in the leaf base, giving a narrower reflexed branch in each basal lobe. Secondary veins anastomosing, forming large open hexagonal or polygonal meshes. Fructification unknown.



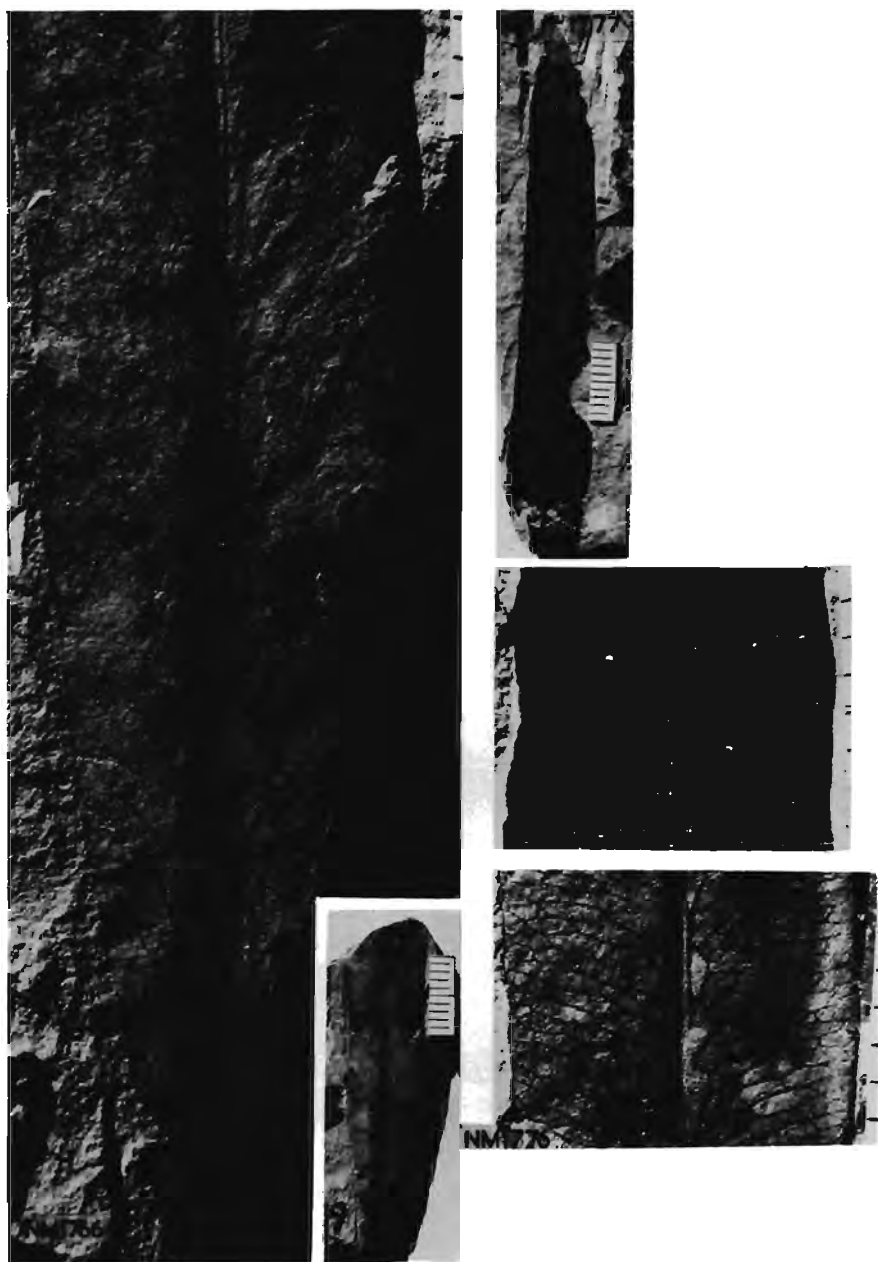
NM 1774 and 1774 enlarged, 1765b: *Glossopteris indica* Schimper $\times 1$ and $\times 5$.



NM 1771: *Glossopteris indica* ('communis' facies) $\times 1$ (*G. communis* Feistmantel).



NM 2010: *Glossopteris angustifolia* Brongniart $\times 1$ and $\times 5$.



NM 1766 and 1766 enlarged: *Glossopteris* cf. *leptoneura* Bunbury $\times 5$ and $\times 1$ (left). NM 1777 and 1777 enlarged, 1776 enlarged: *Glossopteris* cf. *elongata* Dana $\times 1$ and $\times 5$ (right).



NM 1276a, 1754b, 1754a: *Glossopteris conspicua* Feistmantel $\times 2,5$ (left and below). NM 1749: *Glossopteris feistmantelli* ('cordata' facies) Rigby $\times 1$ (*G. cordata* Feistmantel *non* Dana) (top right).



NM 1761, 1775b enlarged: *Glossopteris* cf. *ampla* Dana $\times 1$ and $\times 5$ (cf. *G. damudica* Feistmantel).



NM 1770 enlarged, 1779 and 1779 enlarged: *Glossopteris elongata* Dana $\times 5$ and $\times 1$.

***Belemnopteris elongata* sp. nov.**

Belemnopteris sp. Schopf, J. M., 1970: 63, fig. 5

Specimens figured NM 1743, NM 1750, NM 1748, NM 1751, NM 1741; NM 1772

Specific diagnosis: Leaf elongate or ovate-lanceolate, at least 10 cm long and 3 cm wide, base sagittate, petiolate. Basal lobes acutely or bluntly pointed, at least 7 mm long. Midrib strong, longitudinally striated, 1,5 to 2,5 mm wide, lateral branches about 0,5 mm wide, reflexed, running submarginally on the proximal side of the basal lobes and becoming thinner towards their tips. Secondary veins ascending obliquely at about 45° to the midrib and margin through most of the lamina, but spreading at 90° near the base and downwards into the basal lobes, anastomosing to form an open reticulum, with large slightly elongated hexagonal or polygonal meshes, up to about 3 mm long by 1,5 mm wide, smaller near the margin.

Holotype: NM 1743.

Description: Unfortunately, none of the leaves of *Belemnopteris elongata* in the Mooi River collection is complete. The largest specimen (NM 1741) has a lamina which is 10 cm long and still expanding at the point of fracture. Another (NM 1750) attains a width of 2,8 cm, but is only the basal portion. A third specimen (NM 1743) is nearly complete. It is ovate in its upper part, about 4 cm long by 1,5 cm wide, and the taper suggests that it was bluntly pointed. The specimens thus show a range of size and shape, attaining at least 15 cm long by 3 cm wide, with a pointed apex. In the largest specimens the basal lobes appear relatively less prominent. In all specimens the secondary venation forms a coarse open reticulum very similar to that in *Glossopteris elongata* Dana (see NM 1772).

Both Etheridge (1904) and Du Toit (1932a) point out that leaves with auricles at the base of the lamina do not fall strictly within the original definition of the genus *Glossopteris*. Consequently, NM 1772 is better placed with *Belemnopteris elongata* than included within the limits of *Glossopteris elongata*.

Discussion: *Belemnopteris elongata* is readily distinguished from *B. wood-masoniana*, from the Raniganj stage (Upper Damuda Series) of India, the only other described species in the genus, by its narrow-elongate form, greater length, much shorter basal lobes, and lateral vascular strands running close to their proximal margins.

The new species is strikingly similar to *Belemnopteris* sp., figured (but not described) by Schopf (1970) from Terrace Ridge, Ohio Range, Antarctica. Indeed, Rigby (1973, pers. comm.), who has studied the original Antarctic specimen, states that *Belemnopteris elongata* from Natal and *Belemnopteris* sp. from Antarctica are alike in all essential details.

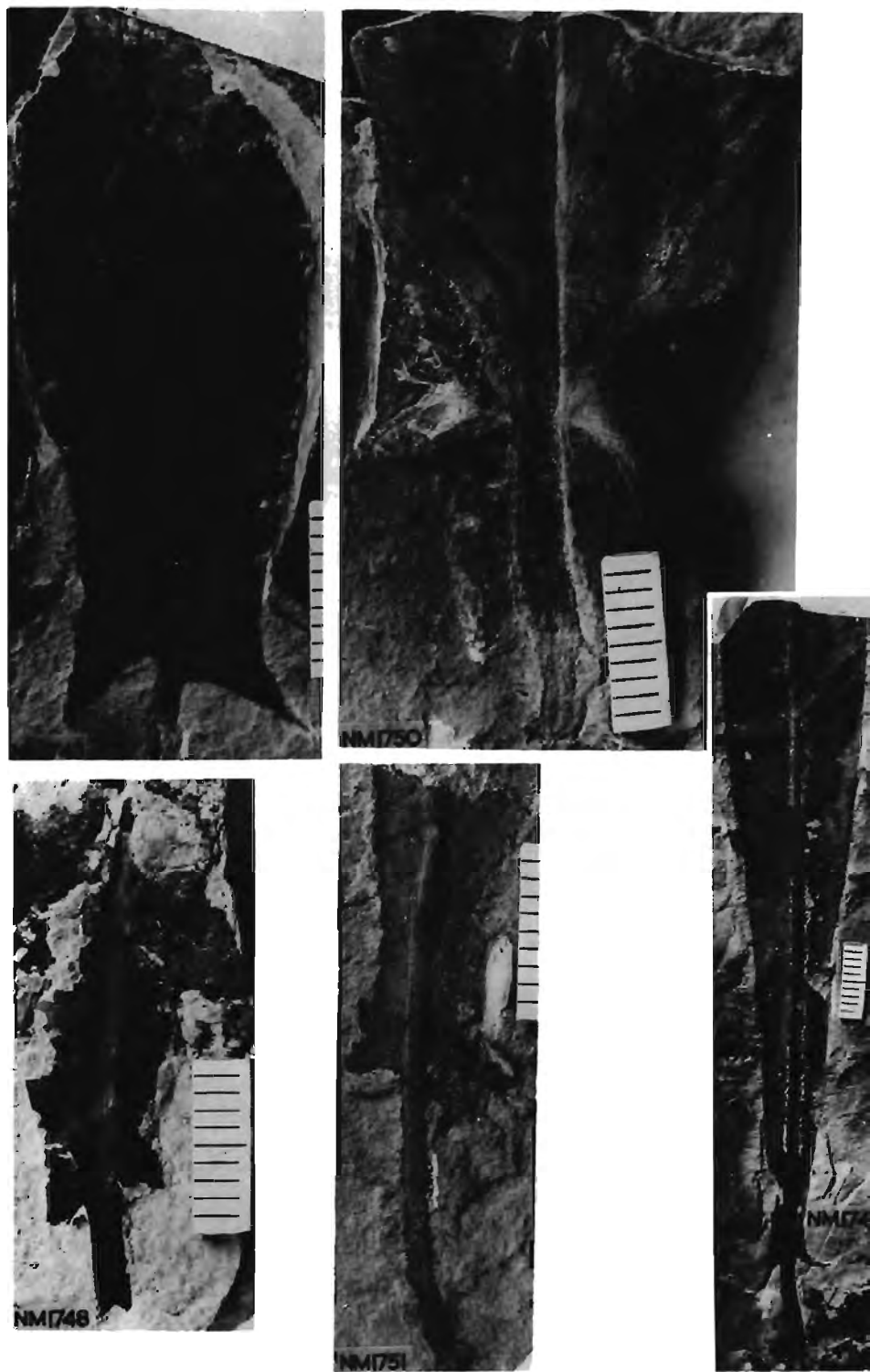
For this reason, *Belemnopteris* sp. is included in *Belemnopteris elongata* sp. nov.

A rather less similar leaf, with wide meshes and sagittate base, from Bald Hill, Bacchus Marsh, Victoria, Australia has been noted by one of us (W.S.L. 1973) in the Natural History Museum, Melbourne, Australia. It may also belong to *B. elongata*.

Scale-leaves

Specimens figured NM 1711, NM 1710, NM 1712, NM 1713, NM 1709, NM 1703; NM 1702, NM 1692b and a

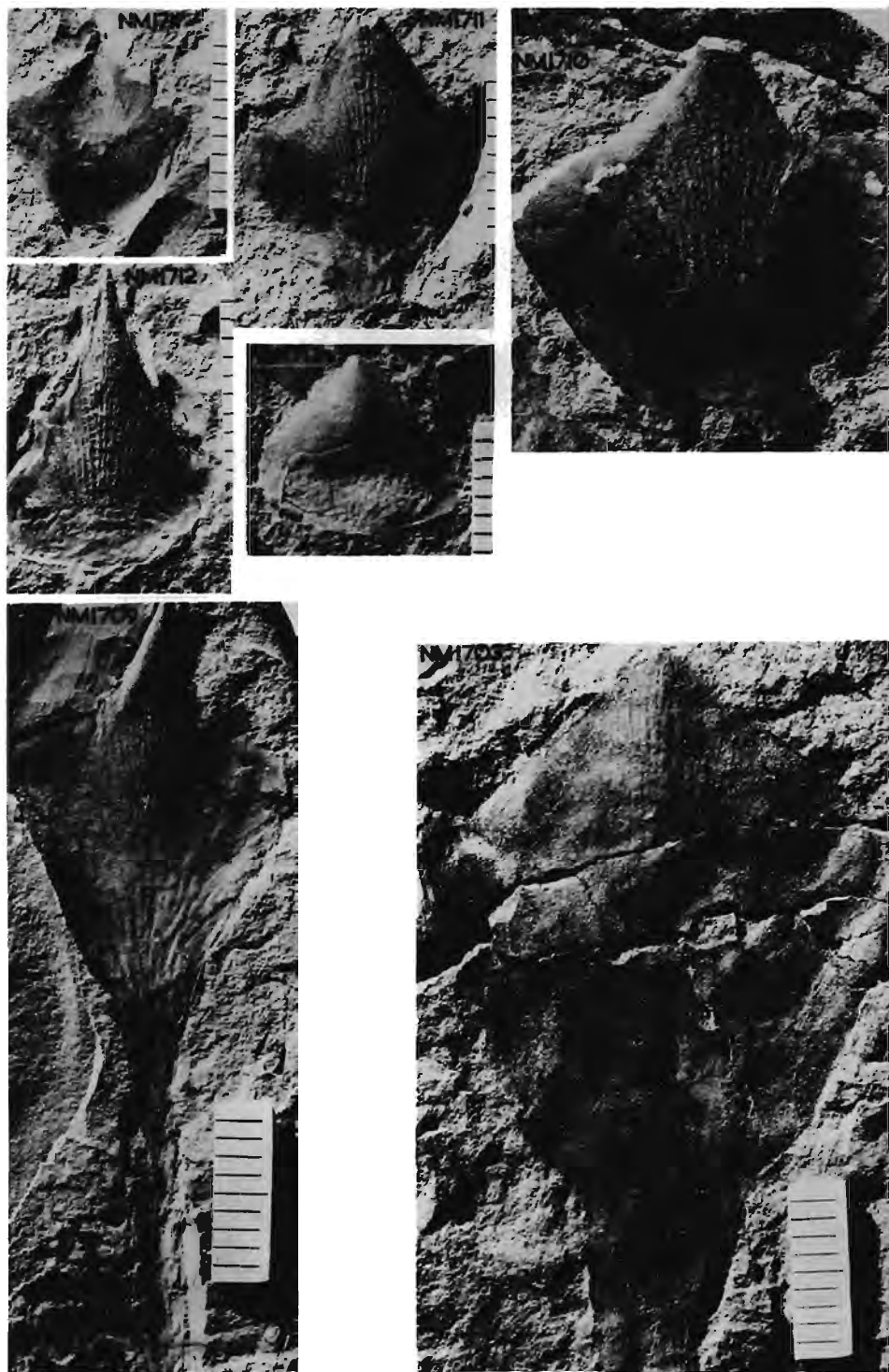
Scale-leaves of many different kinds are abundant in the Mooi River beds. Similar scales occur commonly in the Permian of Gondwanaland and have been recorded



NM 1743, 1750, 1748, 1751, 1741: *Belemnopteris elongata* sp. nov. $\times 2,5$ and $\times 1$.

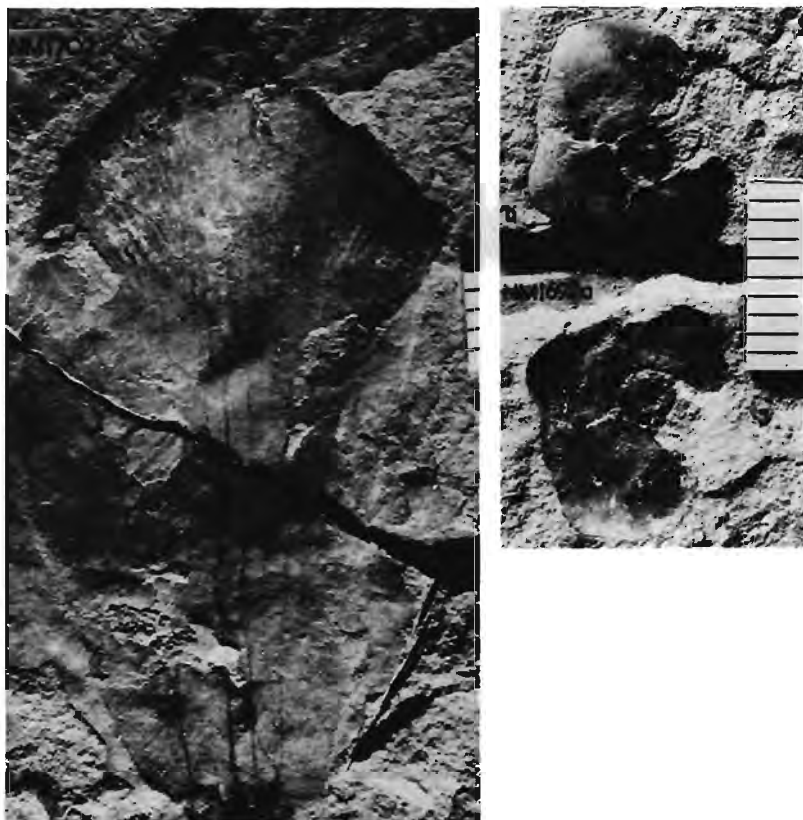


NM 1772 and 1772 enlarged; *Belemnopteris elongata* $\times 1$ and $\times 5$.



NM 1711, 1710, 1712, 1713, 1709, 1703: Glossopterid scale-leaves $\times 2.5$.

many times in the literature (e.g. Arber 1905a; Walkom 1922; Lacey & Kulkarni 1969). They have usually been attributed to *Glossopteris* or *Gangamopteris*, but Rigby (1972b) considers 'that insufficient is known of their relationships to say that they belonged to the same plant that bore leaves of *Glossopteris*'.



NM 1702, 1692b and a: *Glossopteris* scale-leaves $\times 2.5$.

The scale-leaves vary a good deal in size and shape. They are usually detached, but are occasionally found in attached groups of two, three or four (see NM 1692b and a). Rhomboidal scales compare closely with the laminae of *Eretmonia* fructifications; others with a spatulate or ovate shape resemble the fructification *Lidgettonia*; more linear scales resemble some *Glossopteris* leaves.

The heterogeneous assemblage illustrated is regarded as consisting of *Glossopteris* bud-scales from vegetative shoots and of sterile scales from the bases and apices of strobili, the fertile parts of which are probably represented by *Eretmonia* and *Lidgettonia* (see later).

Thomas (1958) has described similar scales from Lidgetton, Natal (the type locality for *Lidgettonia*). They are 2 to 6 cm long, 1.0 to 1.5 cm wide, with a broad base, little or no trace of a midrib, coarse distant veins and fairly frequent anastomoses. It is worth noting that Thomas suggests that these scales were probably organs intermediate between normal photosynthetic leaves and the fertile structure, *Lidgettonia*.

2. Fructifications and Seeds

Genus *Eretmonia* Du Toit (1932) emend.

Type-species: *Eretmonia natalensis* Du Toit, 1932

This genus was established by Du Toit (1932a: 381–386, pl. 40, figs 9–12) for eleven specimens of small paddle-shaped bodies with *Glossopteris* venation from the Lower Beaufort Beds, near Bergville, Natal. Du Toit believed that groups of sporangia were borne in a shallow hollow on the adaxial side of the spoon-shaped distal end of this leaf-like structure, although two of his figures (10, 11) suggest that the sporangia might have been borne laterally on short branches. Lateral attachment has now been shown to occur (Surange & Maheshwari 1970) and is amply demonstrated in some of the new specimens from Mooi River. Surange & Maheshwari (1970) added three more species to the genus and provided a new diagnosis to take account of the new information on sporangial attachment and the range of structure in the four species recognized by them.

However, these authors did not include reference in their new generic diagnosis to the occasionally reticulate venation of the lamina nor did they give details of the sporangia. For these reasons, and because the more than 100 specimens now available in Natal extend the range of structure even more, a further emendation of the genus is necessary.

Emended generic diagnosis: Male fructification, consisting of a stalked fertile leaf bearing pedicellate clusters of sporangia. Very variable in shape and size. Stalk thick to slender, long to very short. Lamina ovate to more or less triangular, occasionally pentagonal, base broad, apex acute to acuminate, venation faint, predominantly dichotomous with occasional anastomoses. Centre of lamina sometimes thick, occasionally with an adaxial depression and accompanying abaxial bulge, margin thinner. Sporangia usually in two pedicellate clusters, one on each side of the stalk near the point of expansion into the lamina. Axis of pedicellate clusters branched several times, with small groups of sporangia on ultimate branchlets. Sporangia very variable in size and number, almost straight to variously curved or reniform, attached by a narrow stalk at one end, wall cells parallel to the long axis of the sporangium, elongated, curved, sinuous or vermiform.

Eretmonia natalensis Du Toit

Syn. *Eretmonia utkalensis* Surange & Maheshwari, 1970

Eretmonia hinjridaensis Surange & Maheshwari, 1970

Eretmonia karanpurensis Surange & Maheshwari, 1970

Specimens figured NM 1212a, NM 1126a, NM 1142, NM 1128b, NM 1129, NM 1160, NM 1189, NM 1222; NM 1221a

The new collection from Natal contains some 120 specimens of *Eretmonia*, though not all of these are complete. They show a considerable range in overall size and shape, and in the number and size of sporangia (see figure). The length of complete specimens ranges from 13 to 50 mm and the maximum width of the lamina from 4 to 24 mm. About one-fifth of the specimens show the shallow depression in the distal end of the lamina noted by Du Toit (1932a) in his original description. The number of apparently connected sporangia visible without excavation of the specimens ranges from 14 to 50, but these figures are not very significant since it is difficult to tell how many more sporangia are embedded in the matrix of specimen and counterpart. Sporangial size

ranges from 1 mm long by 0,5 mm wide to 2 mm long by 0,9 mm wide, the overall range recorded being 1–2 mm in length by 0,4–1,0 mm wide. There is no direct correlation between sporangial size, sporangial number and overall size of the fructification. Small specimens may have a large or small number of sporangia; and sporangial size also varies indiscriminately (see fig. 2). Sporangial size itself, within certain limits, is also probably not very meaningful since size can vary with age and position on a plant.

The dimensions given above include the ranges given by Du Toit (1932a), where the comparable figures are: length, 15 to 35 mm; maximum breadth, 5 to 8 mm; sporangia, 1 to 2 mm long. Du Toit had eleven specimens at his disposal. He considered that the differences, mainly of size, which they showed amongst themselves were probably largely due to growth, for he included them all in the one species, *E. natalensis*. However, he admitted the possibility that the differences might 'in part be specific'. The same questions arise in considering the new Mooi River material. Do the very considerable ranges exhibited represent different expressions of growth in plants growing under different environmental conditions, or in different parts of the same plant, or in different parts of the same male strobilus (assuming that *Eretmonia* male organs were borne aggregated together)? Or are there several species of *Eretmonia* present in the collection?

In an attempt to decide whether stages of growth or different species are represented, about 50 of the best preserved specimens have been plotted graphically and drawn to scale in fig. 2. This composite figure shows not only the distribution of overall sizes, but also variations in shape of the lamina, type of venation, and the incidence of the shallow depression mentioned by Du Toit. Additionally, the inset graph gives data for the sporangia.

Several points are apparent: (1) the specimens show a fairly uniform spread, not falling into disjunct groups, (2) the incidence of an angular lamina, shallow depression in the lamina and anastomosing venation is also scattered, (3) sporangial numbers and size are not directly related to overall size of the specimen.

Until it is possible to correlate *Eretmonias* with named leaf species, these facts justify the conclusion that different growth conditions of one species may be represented. The Mooi River specimens are therefore all referred to *Eretmonia natalensis* Du Toit and are taken as indicating range of growth and form within one species.

Eretmonia has also been described recently from India. Surange & Maheshwari (1970) have established three new species: *E. utkalensis*, based on 'several specimens'; *E. hinjridaensis* and *E. karanpurensis*, based on one specimen each. All three Indian species are said to differ from *E. natalensis* in the shape and size of the fertile leaf and in the number and details of the sporangia. The three species are included in the figure, drawn to scale, for comparison. It will be seen that all three fall within the range accepted in the present account for *E. natalensis*.

Furthermore, (1) there is no material difference in the sporangial sizes as given by Surange & Maheshwari (1970) for their species (*E. utkalensis*, 1,2–1,5 mm long by 0,5–0,8 mm broad; *E. hinjridaensis* 1,3–1,5 mm long by 0,6–0,7 mm broad; *E. karanpurensis*, 1,4–1,6 mm long by 0,5–0,725 mm broad), (2) there is no clear indication of the venation in all three of the Indian species; only in *E. karanpurensis* it is unequivocally stated that there are no anastomoses, and this feature is, in any case, not

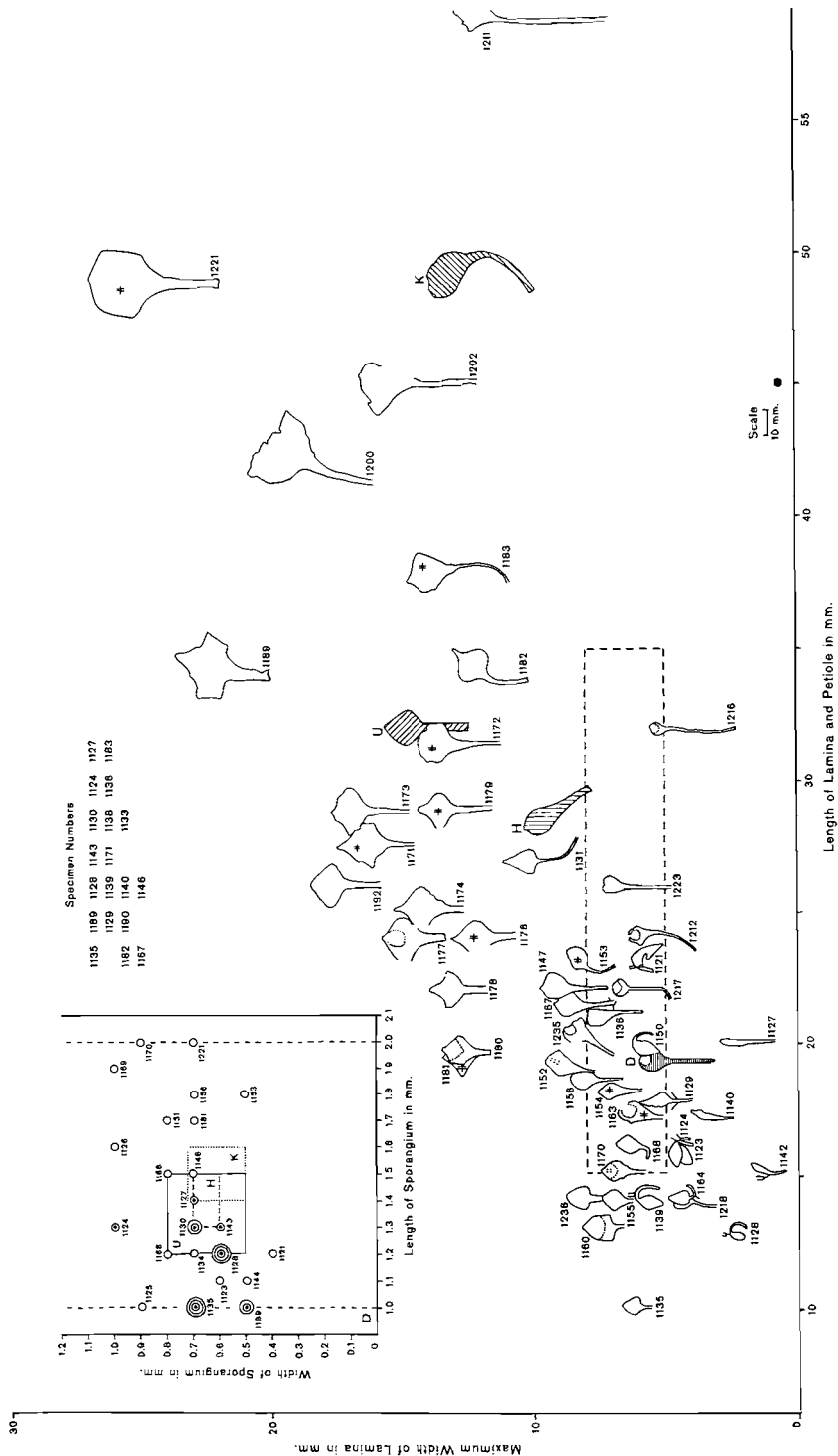





Fig. 2. *Eretmonia natalensis*—microsporophylls.

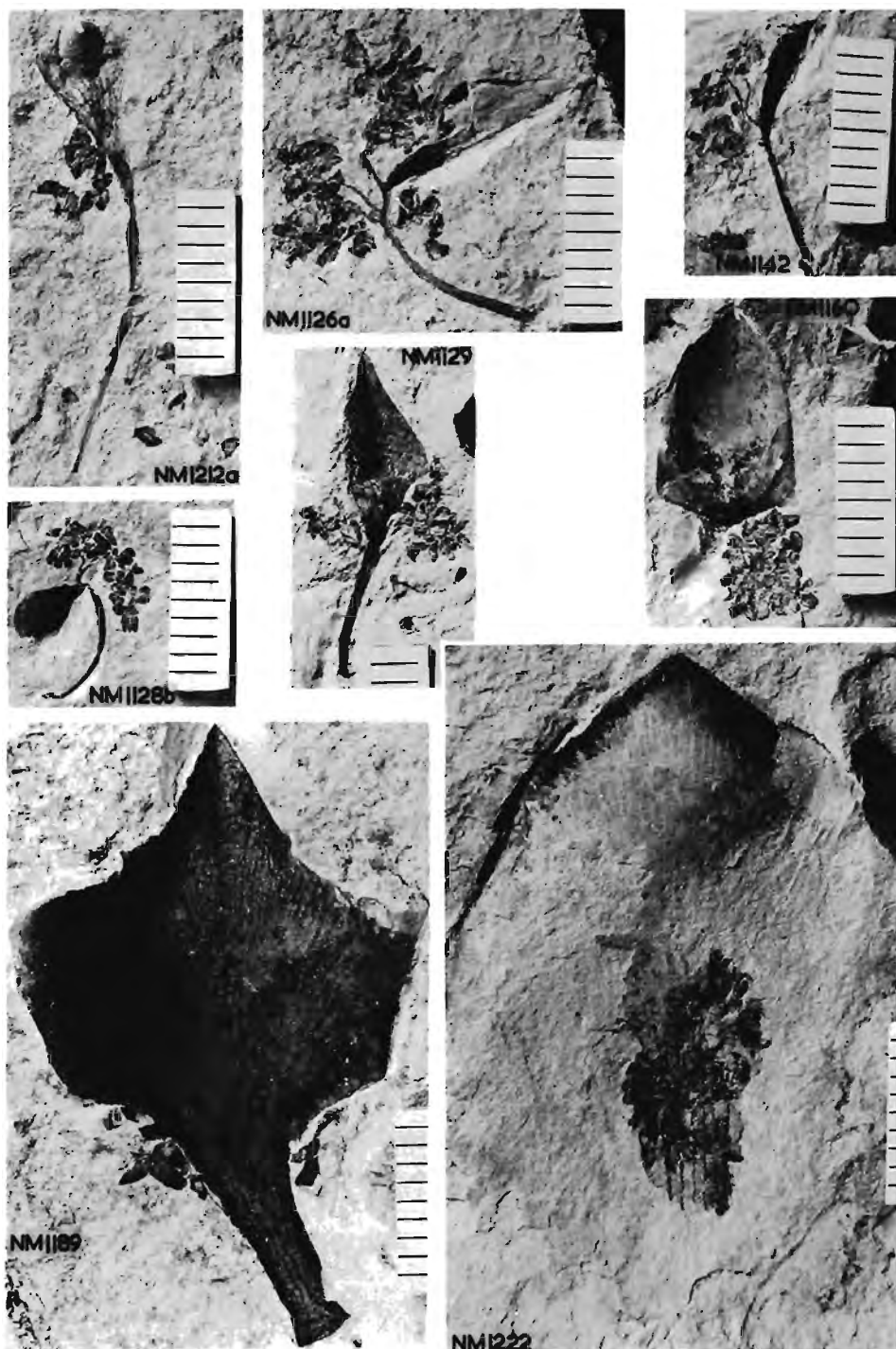
Explanation of figure: accurate outlines of 50 microsporophylls from the Mooi River beds are shown, the position of each on the diagram being determined by its length (abscissa) and maximum width (ordinate). The outlines were drawn to the scale indicated at the bottom right. Pedicels (sporangioophores) were indicated wherever these showed direct (or close) connection with the sporophylls. Each specimen carries its number (NM prefix omitted). In showing detail of the specimens the following symbols signify:

-  — clearly discernible anastomoses in the venation
-  — presence of small depressions (pits)
-  — presence of terminal adaxial concavity or abaxial convexity

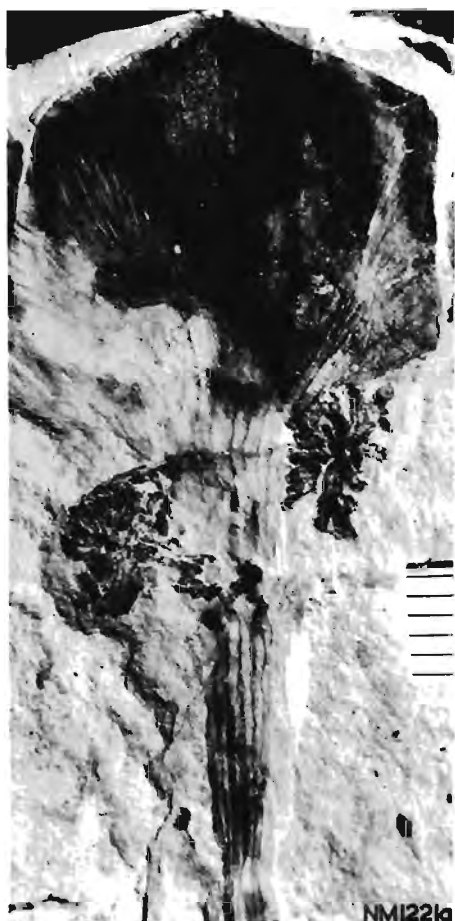
Where the petioles are drawn closed, these are considered complete in the specimens; where left open, these are doubtfully complete. Broken outlines to the sporophylls indicate corresponding gaps in the fossils.

For purposes of comparison, the following were also drawn (according to the dimensions given for the types): *E. karanpurensis* (K); *E. hinjridaensis* (H); *E. utkalensis* (U); *E. natalensis* (D).

Inset: Graph showing range of size of sporangia apparently attached to *Eretmonia natalensis* microsporophylls from the Mooi River beds (36 specimens plotted; numbers of specimens given in graph or in adjacent table: concentric circles indicate sporangia of similar dimensions). For purposes of comparison, the sporangial size range for the following species have also been plotted: *E. karanpurensis* (K) area outlined by dotted line; *E. hinjridaensis* (H) area outlined by broken line; *E. utkalensis* (U) area outlined by continuous line; *E. natalensis* (D) area outlined by dashed line (only length dimensions stated by Du Toit 1932).



NM 1212a, 1126a, 1142, 1128b, 1129, 1160, 1189, 1222: *Eretmonia natalensis* Du Toit $\times 2.5$.



NM 1221a: *Eretmonia natalensis* Du Toit $\times 2,5$ (left). NM 2021: *Arberiella* sp. $\times 25$ (right).

constantly observed in *E. natalensis*, (3) the absence of a shallow depression in the lamina of the Indian specimens is not a reliable distinguishing feature since it is irregular in its occurrence in *E. natalensis* as here understood, (4) the sporangia of *E. karanpurensis* do not appear to differ significantly from those of *E. natalensis* (see photographs). No illustrations of sporangia are given for *E. utkalensis* and *E. hinjridaensis* so comparisons with *E. natalensis* cannot be made.

For the reasons given above, the Indian species *E. utkalensis*, *E. hinjridaensis* and *E. karanpurensis* are here considered as not specifically distinct from *E. natalensis* and they are accordingly included in the latter species.

In the same paper in which they described Indian specimens of *Eretmonia*, Surange & Maheshwari (1970) established a new monotypic genus of male fructifications *Glossotheca*, based on two specimens. Like *Eretmonia*, *Glossotheca* is a stalked fertile leaf of the *Glossopteris* type bearing pedicellate sporangia. The sporangia fall within the range of size of those borne by *Eretmonia natalensis* and are very similar in structure. Surprisingly, Surange & Maheshwari (1970) did not compare *Glossotheca*

with *Eretmonia*, from which it differs by its (1) linear shape, (2) larger size, (3) three pairs of stalked clusters of sporangia borne on a common central stalk, and (4) large number of sporangia (100 ± 20) in each cluster. It is therefore of some interest that the Mooi River collection of *Eretmonias* contains several specimens with more than the usual two pedicellate clusters of sporangia (NM 1126a, NM 1142, NM 1128b). Although it cannot be shown that these clusters arise from a common central axis as in *Glossotheca*, such specimens may serve to link *Eretmonia* with *Glossotheca*. *Eretmonia* and *Glossotheca* represent two related types of male fructification which can be assigned to *Glossopteris* with reasonable confidence, a view also held by Surange & Maheshwari (1970).

Genus *Arberiella* Pant & Nautiyal

Specimen figured NM 2021

In the matrix are many microsporangia that are either isolated as solitary units, or grouped into clusters often without apparent attachment either to one another or to an organ on which they could have been borne. The majority appear identical in size and form with those attached to *Eretmonia* sporophylls. Occasionally, however, a few appear different, either longer, or wider, or with an imprint of larger cells over the wall surface. Such specimens warrant further study, especially attempts to determine whether connections to sporangiophores or sporophylls existed. It is hoped this may form the subject of a subsequent investigation.

Genus *Lidgettonia* Thomas, 1958, **emend.**

Type-species: *Lidgettonia africana* Thomas, 1958

In his original account of *Lidgettonia* Thomas (1958) included simple lanceolate sterile *Glossopteris* leaves, resembling *G. communis* Feistmantel, in the generic diagnosis, because he believed that only one kind of leaf was present in the material at his disposal. Surange & Maheshwari (1970) doubted 'whether the sterile leaves assigned to *Lidgettonia* by Thomas actually belonged to it'. Even if Thomas was right, his action has made it difficult to use the genus *Lidgettonia* for similar reproductive structures occurring without leaves, or with *Glossopteris* leaves of a type other than *G. communis*, or with several different *Glossopteris* species (as in the case of the Mooi River collection). A better course of action would have been to restrict the use of the name *Lidgettonia* to the fertile leaves bearing reproductive structures, as did Du Toit (1932a) in the case of *Eretmonia*.

In practice this restricted conception of the genus *Lidgettonia* has been adopted by several workers (Surange & Maheshwari 1970; Surange & Chandra 1973c). The same restricted view of the genus is taken in the present account. There is justification for this action since (1) Thomas himself selected a single specimen which was a 'fertile leaf with remains of cupules on either side of the petiole' as the holotype of his species *Lidgettonia africana*, which was in turn the type-species of the genus *Lidgettonia*, (2) an examination of new material recently collected from the type locality at Lidgetton, some 40 km from Mooi River, suggests that more than one kind of leaf may be present, (3) the restricted conception of the genus is more convenient in use (although it is realized that this last point is not a sound taxonomic argument).

In view of the usage adopted here, and of additional data presented below, an emended generic diagnosis is required.

Emended generic diagnosis: Female fructification; fertile leaf with seed-bearing cupules. Lamina lanceolate, ovate-lanceolate or spatulate, contracted at the base to form a petiole; midrib absent; veins spreading from the base, forking and sometimes anastomosing to form a coarse network. Cupules usually in two longitudinal rows arising from the abaxial (?) surface of the basal part of the leaf, commonly numbering four to eight, but possibly as many as fourteen, stalked, open campanulate, sometimes appearing semicircular when compressed laterally or disc-like when compressed dorsiventrally, up to about 7 mm in diameter, marked with fine striations radiating from the centre, margin variously lobed, crenate or acutely toothed, with about six to ten lobes or teeth; seeds samaropsid, almost round, 2 to 3 mm in diameter, winged, attached to distal surface of cupule, probably only one or two per cupule reaching maturity.

Lidgettonia africana Thomas

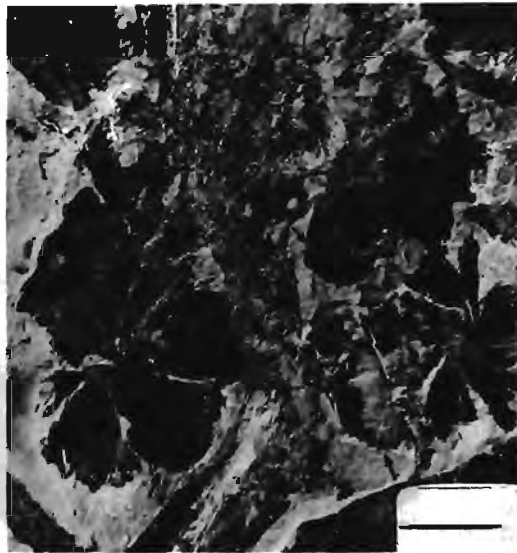
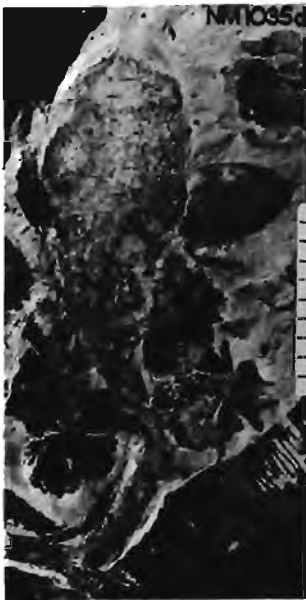
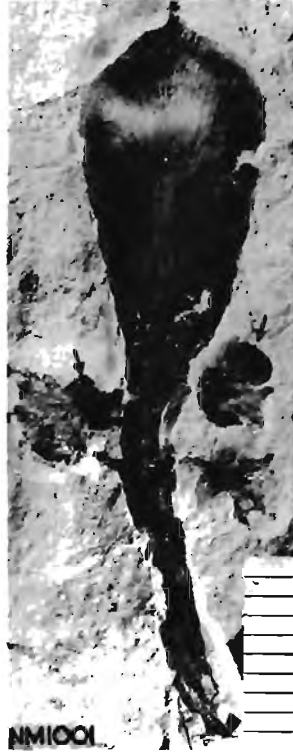
Specimens figured NM 1596a, NM 1001, NM 1051b, NM 1035a; NM 1040a and b, NM 1098b, NM 1002, NM 1066

The original description of this species from Lidgetton, Natal appears to have been based on the study of a rather small amount of material. Seven specimens, all incomplete, are mentioned by Thomas (1958). Their description is somewhat unsatisfactory, as conflicting or ambiguous statements appear in the text. For example, on p. 181 of the 1958 paper, Thomas writes of 'two longitudinal rows of four to six cupules', which implies a total of twelve cupules, while on p. 184 the description of a specimen with six or possibly seven cupules on one margin, with indications of two or three on the other, might suggest a total of fourteen cupules. The quality of the illustrations is insufficient to resolve these uncertainties. In view of these difficulties, new material has been collected recently from the type locality at Lidgetton and the information available from this has been incorporated in table 2 with data given by Thomas (1958).

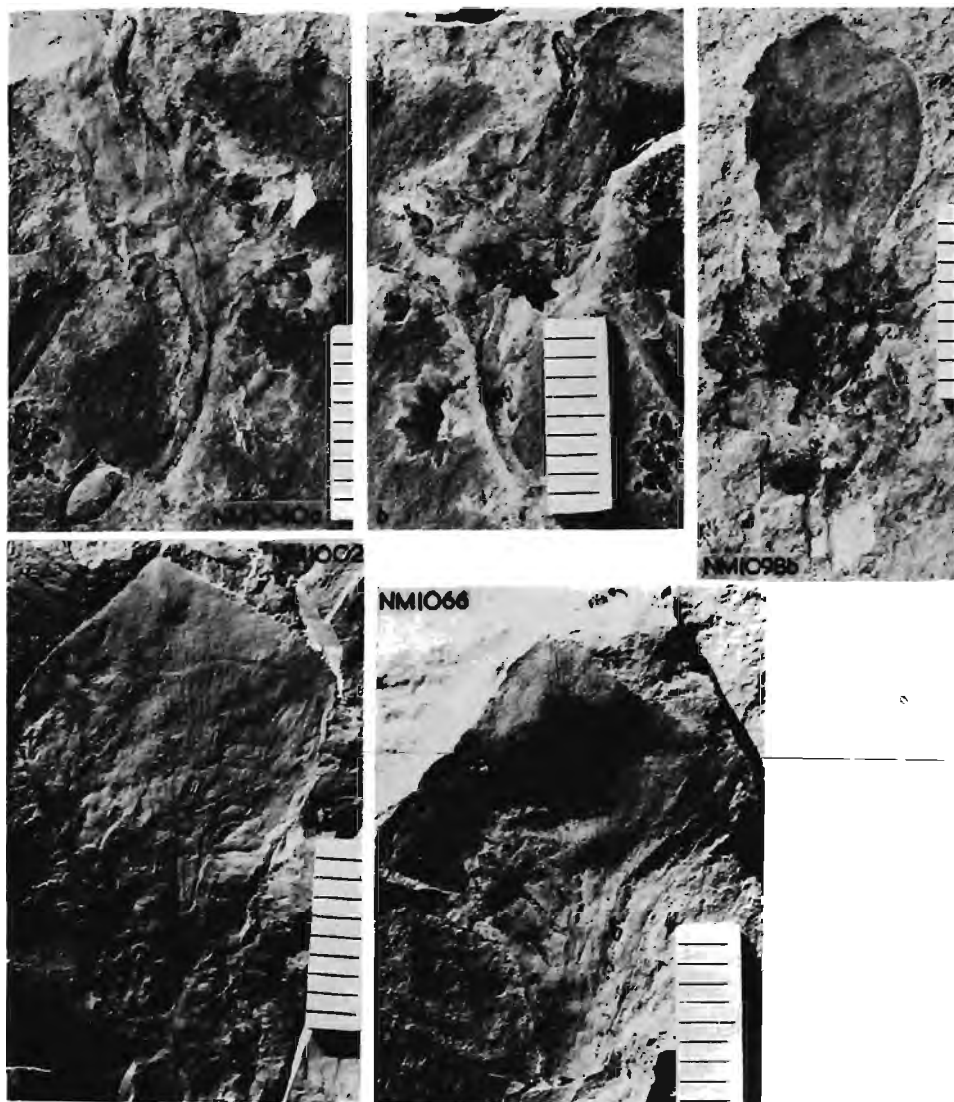
The Mooi River collection contains some 120 specimens of *Lidgettonia*, most of which can be referred with confidence to *L. africana*. For comparison, data from 50 well-preserved specimens are given in table 2.

TABLE 2
Lidgettonia africana Thomas

| Features | Lidgetton material (10 specimens) | Mooi River material (50 specimens) |
|---|---|---------------------------------------|
| Overall length | 3,0 to 4,5 cm (but no complete specimens available) | 2,2 to 4,0 cm |
| Width of lamina | 1,2 to 1,5 cm | 0,6 to 1,7 cm |
| Width of petiole base | 1,5 to 3,0 mm | 0,7 to 3,0 mm |
| Number of cupules per fertile leaf | usually 4 to 8 (but perhaps up to 14) | usually 2 to 4 (sometimes 5 to 7) |
| Width of cupules (measured in dorsiventrally flattened specimens) | 5 to 7 mm | 4,0 to 7,5 mm |
| Number of cupule lobes | 6 to 10 | 6 to 11 |
| Length of cupule stalk | about 5 mm | about 4 mm |
| Width of cupule stalk | 0,6 to 0,7 mm | 0,2 to 1,0 mm |
| Diameter of associated seeds | 2 to 3 mm | 2 to 3 mm |



NM 1596a, 1001, 1051b, 1035a and 1035a enlarged: *Lidgettonia africana* Thomas $\times 2,5$ and $\times 5$.



NM 1040a, 1040b, 1098b, 1002, 1066: *Lidgettonia africana* Thomas $\times 2.5$.

BELOW: Line tracing showing sporophyll with numerous cupules (NM 1098b); three sporophylls in abaxial aspect (?) showing the course of the stalks that bear cupules (NM 1040b, 1002, 1066).

The close agreement between the Lidgetton and Mooi River material fully justifies the inclusion of the latter in *L. africana*. There is some indication that the Mooi River specimens are slightly smaller in overall size and had fewer cupules.

In his description of the Lidgetton material Thomas (1958) mentioned the occurrence of 'many isolated seeds in close proximity to the sterile and fertile leaves' and added that in two instances the seeds were in close contact with cupules. Thomas suggested that these seeds may have been extruded from the cupules when they were compressed during fossilization. Of the fifty selected Mooi River specimens, thirty have seeds in close proximity; ten of these have the appearance of having been squeezed from cupules, and five others are partly overlapped by cupules. The foregoing is revealed by development of the specimens. As far as can be seen, these seeds are actually attached to the cupules. One particularly instructive specimen, NM 1035a and b, has three attached seeds, two of them in one cupule. In these latter the micropyle is, in both cases, directed outwards.

The seeds are of the *Samaropsis* type (NM 1001, 1035a, 1002). They are almost circular, ranging from about 2 mm wide by 1,6 mm deep to 3 mm wide by 2,8 mm deep overall, with a central oval sclerotesta ranging from about 1 mm long by 0,8 mm wide to 2,5 mm long by 1,2 mm wide, surrounded by a wing 0,6 to 1,0 mm wide. The wing shows an indentation at the micropylar end of the seeds, but scarcely extends across the base, which appears flattened or truncate. In favourably preserved specimens such as NM 1035 a pattern of large isodiametric cells is visible on the wings, and one of narrow, vertically elongated cells on the sclerotesta.

The seeds agree in all respects with those described by Thomas (1958) from Lidgetton.

There can no longer be any doubt that *Lidgettonia africana* was a cupulate seed-bearing structure.

Discussion: Several seed-bearing Glossopterid fructifications from the Lower Gondwana of India described by Surange & Maheshwari (1970) and Surange & Chandra (1973b, c) have, according to their account, some similarity to *Lidgettonia africana*. One of these, first described as *L. indica* (Surange & Maheshwari 1970), subsequently formed the basis of a new genus, *Partha* (Surange & Chandra 1973c), with two species, *P. indica* (Surange & Maheshwari) Surange & Chandra and *P. spathulata* Surange & Chandra. These fructifications are not as yet well understood. Surange & Chandra (1973c) themselves could not decide whether their two to four pedicellate organs bear one to four single-seeded cupules at the distal end of each pedicel or one peltate or disc-like cupule with one to four large seeds. This uncertainty makes comparison with *Lidgettonia africana* difficult, but, if the description of the genus *Partha* given by Surange & Chandra (1973c) is correct, it can be distinguished from *Lidgettonia* by (1) its different shape, (2) the attachment of its pedicellate cupules in a cluster or in one row, rather than in two rows, and (3) in having either solitary disc-like several-seeded or clustered single-seeded cupules, neither of which were campanulate.

A second new genus, *Denkania*, with one species, *D. indica*, described by Surange & Chandra (1973b) bears five or more probably single-seeded oval-lobed cupules on long slender pedicels. They are said to occur in a single longitudinal row both at the base of the lamina and also on the petiole. *Denkania* is thus clearly distinct from *Lidgettonia* both in the structure of individual cupules and in the manner in which

the cupules are borne.

Despite the differences mentioned above, it seems probable that *Lidgettonia*, *Partha* and *Denkania* are related genera of Glossopterid seed-bearing fructifications.

***Mooia lidgettonioides* gen. et sp. nov.**

Specimens figured NM 1476b, NM 1479b and a, NM 1471a, NM 1533, NM 1539, NM 1576b, NM 1579, NM 1474

The collection contains some 50 specimens of a cupulate, probably seed-bearing fructification which resembles *Lidgettonia* in some respects, but the form of the cupule and its associated non-samaropsid seed provide sufficient reason for excluding it from that genus. The new genus *Mooia* (pronounced 'Moyia') is proposed for it, derived from Mooi River, so far its only known locality. The specific name *lidgettonioides* refers to its general likeness to *Lidgettonia*.

Combined diagnosis: Female fructification consisting of a petiolate fertile leaf bearing two to four stalked, usually drooping, campanulate cupules. Overall length about 1,0 to 2,3 cm. Lamina spatulate or more or less rhomboidal, up to 0,7 cm wide, venation dichotomous, occasionally anastomosing, midrib absent, narrowing into a massive petiole or petiole-like part up to three-quarters of the overall length and 2 mm in width. Lamina sometimes with a distal, abaxially convex, adaxially concave, spoon-shaped depression up to 6 mm long by 5 mm wide, surrounded by a narrow margin of thinner texture. Two to four cupule-bearing pedicels, borne adaxially on the distal part of the petiole or proximal part of the lamina, attached singly or in pairs or possibly more than two together, apparently in a single, longitudinal row. Pedicels unbranched, up to 1 cm long, 0,3 to 0,8 mm wide. Cupules solitary on the pedicels, often reflexed and drooping, variable in size, lobed, from 3 to 8 mm across when seen in profile, to 11 mm from lobe tip to lobe tip when compressed dorsiventrally. Cupule lobes four to eight, from 3,0 to 6,5 mm long and 1 to 2 mm wide, longitudinally striated with a fairly well-defined midline, acutely pointed, fused basally to form the 'cup' of the cupule, often appearing to be in a spiral sequence rather than a whorl. Seed flattened, scarcely winged, about 4,2 mm long and 3,2 mm wide, probably only one per cupule.

Syntypes: NM 1471, 1476, 1576.

Description and discussion: *Mooia lidgettonioides* is regarded as a female fructification since in one case there appears to be organic connection between a seed and a cupule (NM 1471a) and in a few other cases similar seeds lie in close relationship with cupules, correctly orientated for attachment to have been possible.

The fructifications are of similar construction to those of *Eretmonia natalensis*. With few exceptions, they are of comparable size. Furthermore, some exhibit adaxially the spoon-shaped depression at the distal end of the lamina and thus resemble, in particular, the slender oblanceolate sporophylls described by Du Toit (1932a) as typical of *E. natalensis*.

There is also homology with *Lidgettonia africana*, specimens of which are abundant in the Mooi River collection. The latter differ in their more massive sporophylls, differently shaped cupules, and different type of seed. It is worth noting that, while Thomas (1958) did not mention a spoon-shaped area on the lamina of *Lidgettonia africana*, more recent collections from the type locality (Plumstead 1969: pl. 17, fig. 3;

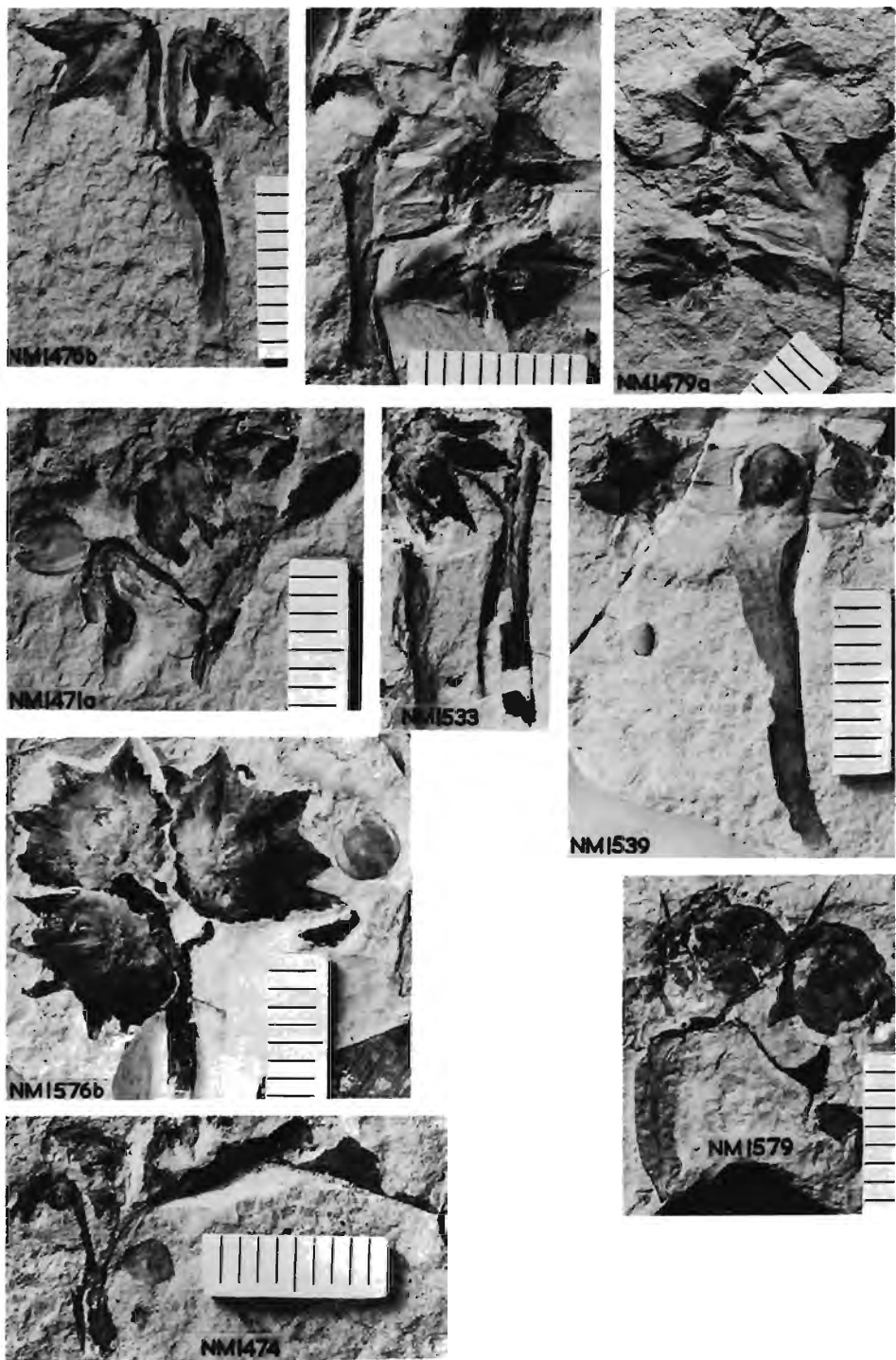
and Van Dijk specimens in the Natal Museum) include specimens that show this feature. Its true nature is not yet understood, thus its significance as an expression of relationship cannot be estimated. If it is the result of the fossilization process, it must be discounted in considering relationships, but, if it represents a special feature of some only of the sporophylls produced by a plant, then it may or may not be indicative of affinity. Its presence on only a few of the sporophylls of *Eretmonia natalensis*, *Lidgettonia africana* and *Mooia lidgettonioides* is thus insufficiently reliable evidence for relating these fructifications as, perhaps, micro- and megasporangiate organs of one species of a genus and the megasporangiate organ of a second species of the same genus respectively.

The specimens of *Mooia lidgettonioides* are also interesting in that there appear to be stages in development of the reproductive organs represented. Some (for example NM 1474) show a rather small sporophyll carrying what appear to be immature cupules of varying age. In this specimen the smallest (youngest ?) cupule is developed on a short pedicel arising from the same point as does a longer, stouter pedicel carrying a larger (older ?) cupule.

This suggests that the reproductive units may have developed in sequence from each point of origin. (Incomplete specimens exist where the cupules appear to have been detached from their pedicels before, or during, fossilization: these, studied in isolation, are likely to be interpreted as carrying pedicels that are paired, or grouped, since age differences are not clear.) The points of origin of the cupules appear to have been situated in a longitudinal row (or rows ?) on the adaxial surface of the sporophyll. Younger cupules appear fluted or folded, often giving the impression of consisting of overlapping veined scales arranged in spiral sequence on the broadened apex of a pedicel and pendant from this, so that an illusion is given of a shaggy membranous-drooping fructification (for example NM 1533 and 1579). Mature cupules are more clearly cup-shaped and in the best-preserved specimens it is possible to see that there is a 4-8 lobed cupular structure represented, the lobes being more or less triangular in shape, each with an acute apex (for example NM 1476, 1479, 1576). In specimens where the cupules are large and believed to be mature, a sporophyll is often lacking: what is represented appears to be the pedicels, either paired (NM 1476), or attached separately (NM 1533, 1576) to a stouter organ that could represent a common stalk or, what is probably more likely, is the petiolar portion of a more massive sporophyll, the lamina of which is either sunken in the matrix as is suggested by some specimens (NM 1476), or shrivelled, or broken away. It seems clear from the dimensions of the mature cupules and the number borne in close association, that a reasonably massive sporophyll (with fairly large lamina ?) would be required to support them. The pedicels appear to have organic connection with the petiole-like part, being clearly decurrent upon it in some cases (NM 1533).

Where laminae are present, the sporophylls of which they form part are all small and rather slender, one in particular (NM 1539) resembling Du Toit's type-specimens of *E. natalensis*, but carrying two cupules extending to left and right of the spoon-shaped apex. Like the sporophylls of *Eretmonia*, the venation is generally dichotomous, but reticulations can be found, especially in the larger laminae: thus these fructifications can be related to *Glossopteris*.

The seeds associated with the cupules are not broadly winged nor of typical sama-



NM 1476b, 1479b, 1479a, 1471a, 1533, 1539, 1576b, 1579, 1474: *Mooia lidgettonioides* gen. et sp. nov. $\times 2.5$.

ropsid shape. Thus they clearly differ from the seeds found in connection with the cupules of *Lidgettonia africana* in form, in their larger dimensions and in their different length/breadth ratio. The seed-bearing appendages themselves also differ in form, being reflexed and cupulate in *Mooia lidgettonioides*, more disc-like with up to eleven smaller lobes in *Lidgettonia africana*. There also appear to be differences in the position of attachment to the sporophyll (adaxial in *Mooia*; abaxial in *Lidgettonia*), but this is not yet fully proven. There are also often fewer appendages to a sporophyll in the former as compared with the latter. No other known megasporangiate fructifications of the *Glossopteris* Flora relate closely to the specimens here described as *Mooia lidgettonioides*.

***Rusangea elegans* gen. et sp. nov.**

Specimens figured NM 1362b and a, NM 1363a, NM 1361a and b, NM 1384 b and a

Twenty-three specimens of another seed-bearing fructification have been recognized in the collection. It consists of a petiolate narrow-ovate fertile leaf, with *Glossopteris*-type venation, and two lateral scale-like projections, each with a single seed, at the base of the lamina. It differs from previously described Lower Gondwana seed-bearing structures and the new name *Rusangea elegans* is proposed for it.

The generic name *Rusangea* is an anagram of *Surangea*, which is preoccupied. It is named for Krishna R. Surange in recognition of his extensive contributions to Indian palaeobotany and for his assistance in the preparation of the present account. The specific name refers to the slender, elegant appearance of the fructification.

Combined diagnosis: Female fructification consisting of a petiolate fertile leaf bearing two scales, each with a single sessile seed, at the base of the lamina. Overall length about 2,5 cm, width of lamina about 0,6 cm, width of petiole base about 0,15 cm. Veins dichotomous, ascending, occasionally anastomosing to form a coarse reticulum with elongated meshes. Scales about 0,3 cm long, arising at the base of the lamina on its adaxial side and continuing beyond the seeds. Seeds two, almost round, about 0,325 cm wide by 0,35 cm long, sessile on the scale.

Holotype: NM 1361.

Description: The 23 specimens of *Rusangea elegans* show marked uniformity of size and form. Most of them are complete. The following details result from analysis of the sixteen best specimens. The shape is consistently that of a narrow-ovate petiolate *Glossopteris* leaf. The overall length ranges from 1,8 to 2,8 cm (mean 2,5 cm), the lamina width from 0,45 to 0,75 cm (mean 0,6 cm) and the petiole width from 0,1 to 0,2 cm (mean 0,15 cm). The venation is clearly visible in more than 50% of the specimens and is coarsely reticulate, with vertically elongated meshes. There is no clear indication of a midrib, but in some specimens the central veins pursue a close parallel course nearly to the apex. In most of the specimens two seed-bearing scales are attached at the base of the lamina on its adaxial side. The seeds are slightly oval in outline and range from 0,3 to 0,4 cm broad (mean 0,325 cm) by 0,3 to 0,45 cm long (mean 0,35 cm). They are not obviously winged.

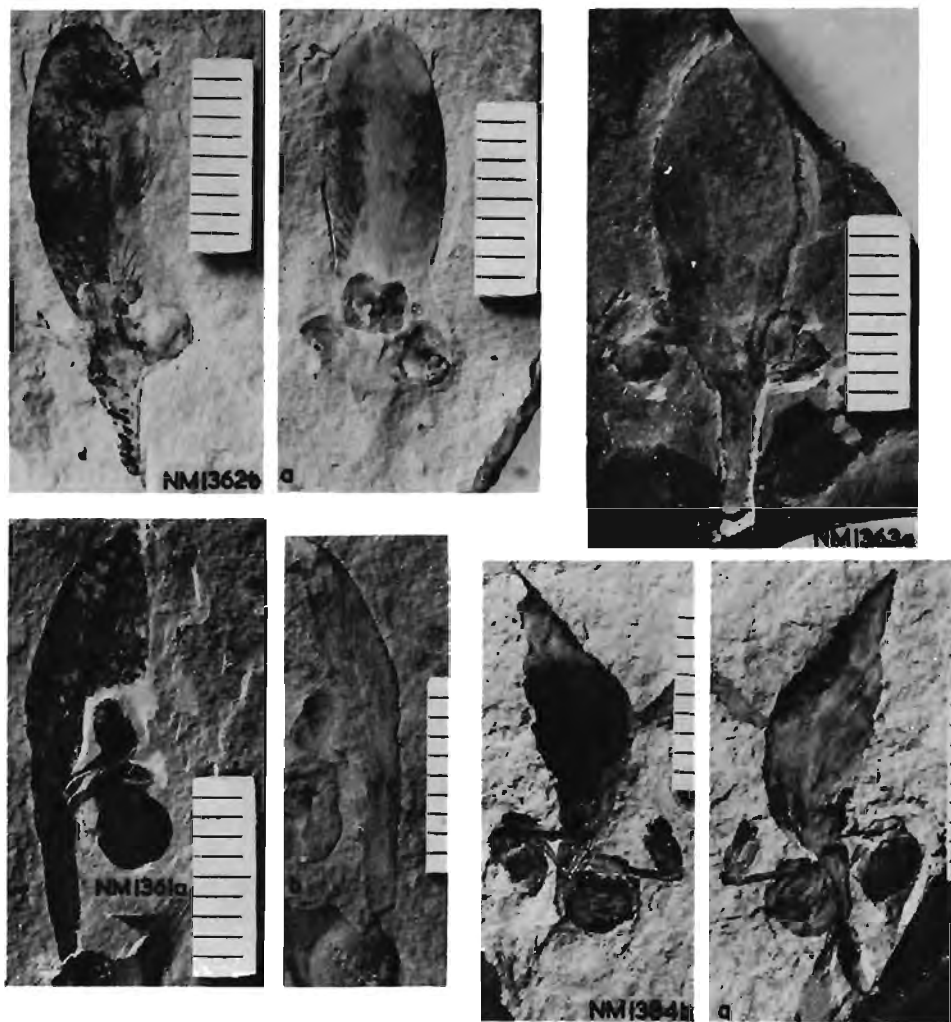
In the best specimen (NM 1361a, b) the seed is borne on a scale, about 0,3 cm long, which extends beyond the seed. Several specimens show only one seed, the other being hidden in the matrix. Some specimens are seen from the abaxial side of the fructification, when attachment is not visible.

Two other forms of this fructification require comment. The specimen NM 1362a, while agreeing in other respects with the majority of the specimens, appears to have *four* sessile seeds or seed-like bodies. This is regarded as showing a juvenile stage, before the seed-bearing scales have extended and unfolded completely.

Another specimen NM 1384a, b has long scales, with the seed detached on one side, and is regarded as a mature condition.

The scales in *Rusangea elegans* are slightly expanded distally, beyond the point of attachment of the seed, but can scarcely be considered cupulate.

Discussion: In Lower Gondwana floras *Rusangea elegans* is readily distinguished from *Lidgettonia africana*, *Partha indica*, *Partha spathulata* and *Denkania indica*, because the latter four taxa all have cupulate seed-bearing structures borne in a different way (see Discussion in the section on *Lidgettonia*, p. 388).



NM 1362b, 1362a, 1363a, 1361a, 1361b, 1384b, 1384a: *Rusangea elegans* gen. et sp. nov. $\times 2.5$.

Of Northern Hemisphere Late Palaeozoic and Early Mesozoic seed-bearing organs, *Rusangea elegans* resembles the Rhaetic megasporophyll *Cycadocarpidium erdtmanni* Nathorst in gross morphology. *Cycadocarpidium* differs in having parallel longitudinal veins in its sterile lamina and very short scale-like projections at the base of the lamina bearing its two sessile seeds.

Cycadocarpidium is associated with *Podozamites* leaves in the Rhaetic of east Greenland and western Europe and is believed to be a conifer or genus intermediate between conifers and cycadophytes (Arnold 1947). *Rusangea* is here regarded as a member of the Glossopteridales, but does possess suggestive resemblances to conifer and cycadophyte female cone scales.

Genus *Scutum* Plumstead, 1952

Scutum conspicuum* **comb. nov., attached to *Glossopteris conspicua* Feistmantel

Specimens figured NM 1276a and b

Six specimens of leaves referable to *Glossopteris conspicua* Feistmantel have been found. Their identification has been confirmed by J. F. Rigby and K. R. Surange (pers. comm.). In one instance a fructification of the *Scutum* type is attached. This differs from *Scutum draperium* Plumstead previously referred by Plumstead (1952, 1956, 1958) to *Glossopteris conspicua* leaves and appears to be new.

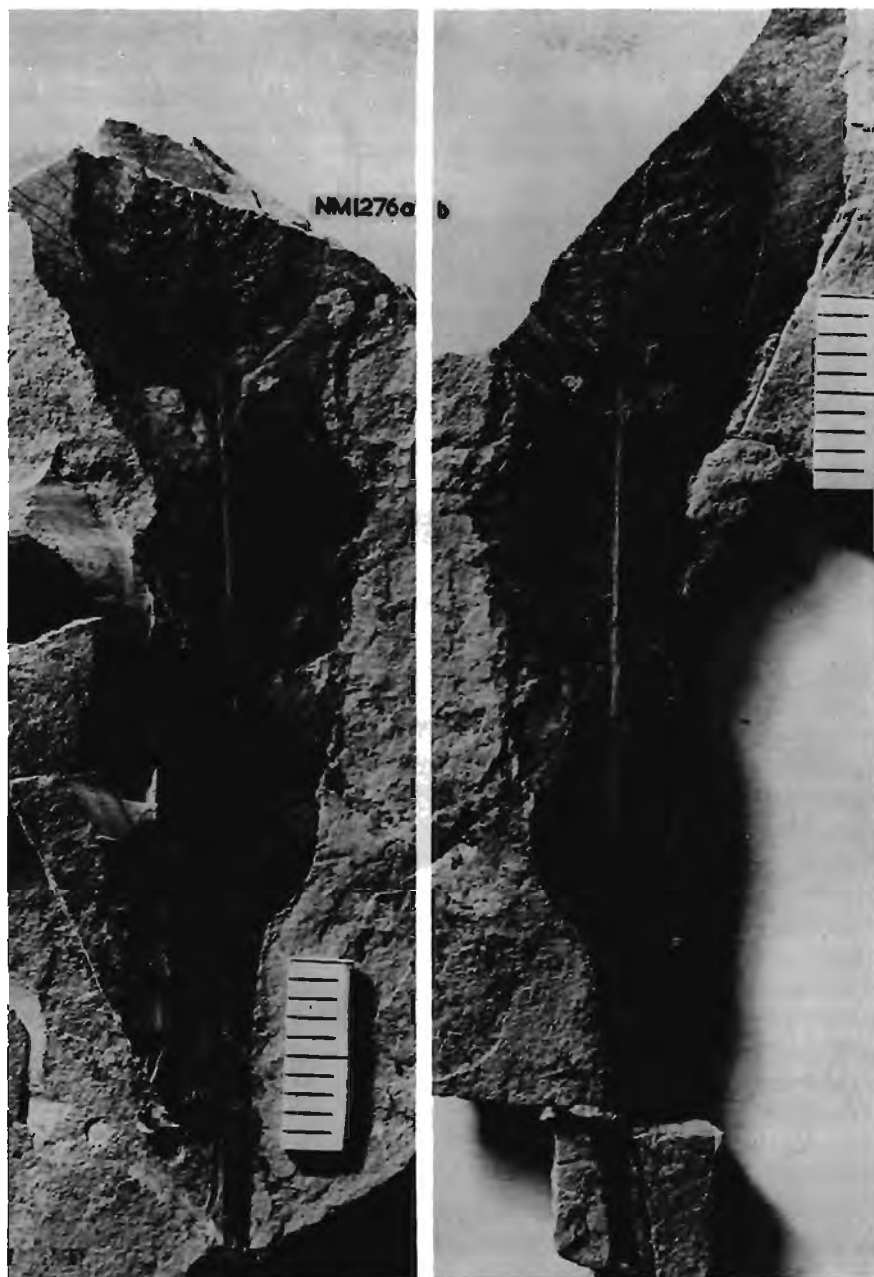
Specific diagnosis: Shield-shaped fructification, oval, 14 mm long by 12 mm wide; central body about 11 mm long by 8 mm wide, marked with about 75 rounded scars, each approximately 0.5 mm in diameter; wing 3 mm wide at apex, reducing to 2 mm wide at the sides, narrowing and slightly decurrent at the base, flat, scarcely striate, probably thin, margin entire; fructification apparently sessile, attached by a conspicuous band of tissue which arises near the centre of the fructification and increases to 2 mm wide below, confluent with the midrib of a *Glossopteris conspicua* leaf about 3 cm above junction of lamina and petiole.

Holotype: NM 1276.

Discussion: A fructification attributed to *Glossopteris conspicua* Feistmantel has been previously described by Plumstead (1952, 1956, 1958) as *Scutum draperium*. This species was based on five specimens, of which three were attached to leaves. It differs markedly from *Scutum conspicuum* (1) in its much larger size, being about 3.8 cm long by 3.2 cm wide, (2) in its large head with very small and numerous scars, (3) in its relatively narrow, fluted wing, and (4) especially in the position of attachment at the base of the leaf blade.

It is unlikely that the same leaf species would have borne different fructifications attached differently in various specimens. The probable explanation of this situation is to be found in a statement by Banerjee & Ghosh (1972) that 'the fertile leaves described by Plumstead from South Africa . . . as *G. conspicua* (bearing *Scutum draperium* Plumstead type of fertile organs) . . . are . . . not properly identified'. Since the identification of the Mooi River leaves as *Glossopteris conspicua* has been confirmed by two independent authorities, *Scutum conspicuum* is here regarded as the true fructification of *Glossopteris conspicua* Feistmantel. This implies that the Middle

* Should the fructification of the type-species of *Glossopteris* prove to be of the *Scutum* type, the genus *Scutum* will fall into synonymy under *Glossopteris*.



NM 1276a, 1276b: *Scutum conspicuum* comb. nov. $\times 2.5$.

Ecce Vereeniging leaves of Plumstead (1952, 1956, 1958) represent a different species and is more in line with the view taken by Du Toit (1954) that *Glossopteris conspicua* is characteristic of Lower Beaufort or even higher horizons.

Genus *Plumsteadia* Rigby, 1963***Plumsteadia natalensis* sp. nov.**

Specimens figured NM 1260, NM 1243a and b, NM 1265, NM 1274a and b, NM 1257

About 30 specimens of a fructification of the *Scutum-Hirsutum-Plumsteadia* type (Plumstead 1952, 1956, 1958; Rigby 1963, 1968) have been found in the Mooi River shales. They appear to combine some of the features found in all three genera and in addition have some similarity to *Dictyopteridium* Feistmantel. For these reasons, they have proved difficult to classify. However, the new specimens appear to be bifacial organs, which excludes them from *Dictyopteridium*, shown recently by Surange & Chandra (1973a) to be a stalked linear-lanceolate cone, with seeds attached on cushions all round the cone axis. Further, they do not possess the well-marked membranous wing characteristic of *Scutum* or the hair-like pollen organs ascribed by Plumstead to *Hirsutum*; they are therefore placed provisionally in the genus *Plumsteadia* Rigby as a new species. *Plumsteadia* Rigby replaces *Cistella* Plumstead, which was preoccupied (Rigby 1963, 1968).

Most of the specimens are detached, but three show attachment to narrow *Glossopteris* leaves.

Specific diagnosis: Bifacial fructification attached to the midrib of a narrow *Glossopteris* leaf of the *indica-angustifolia* type on its adaxial side at or near the base of the lamina. Fructification a flattened, ovate-lanceolate scale, base rounded, apex pointed, 18 to 28 mm (mean 21 mm) long, 7 to 12 mm (mean 8 mm) wide, about 0,25 to 0,5 mm thick, basal attachment scar crescentic, about 2 mm wide. Fructification bearing closely packed raised bodies or sacs on its adaxial face. Sacs arranged in rows which curve upwards and outwards from the centre to the margin, each sac marked with a scar varying from circular, not contiguous, about 0,5 mm wide, to angular, contiguous, about 1 mm wide, both forms with an outer raised rim, middle depression and central raised boss. Outer sides of the marginal sacs vertical in uncompressed specimens, often sloping inwards in compressed specimens, giving the appearance of a narrow reflexed wing, but no true wing present.

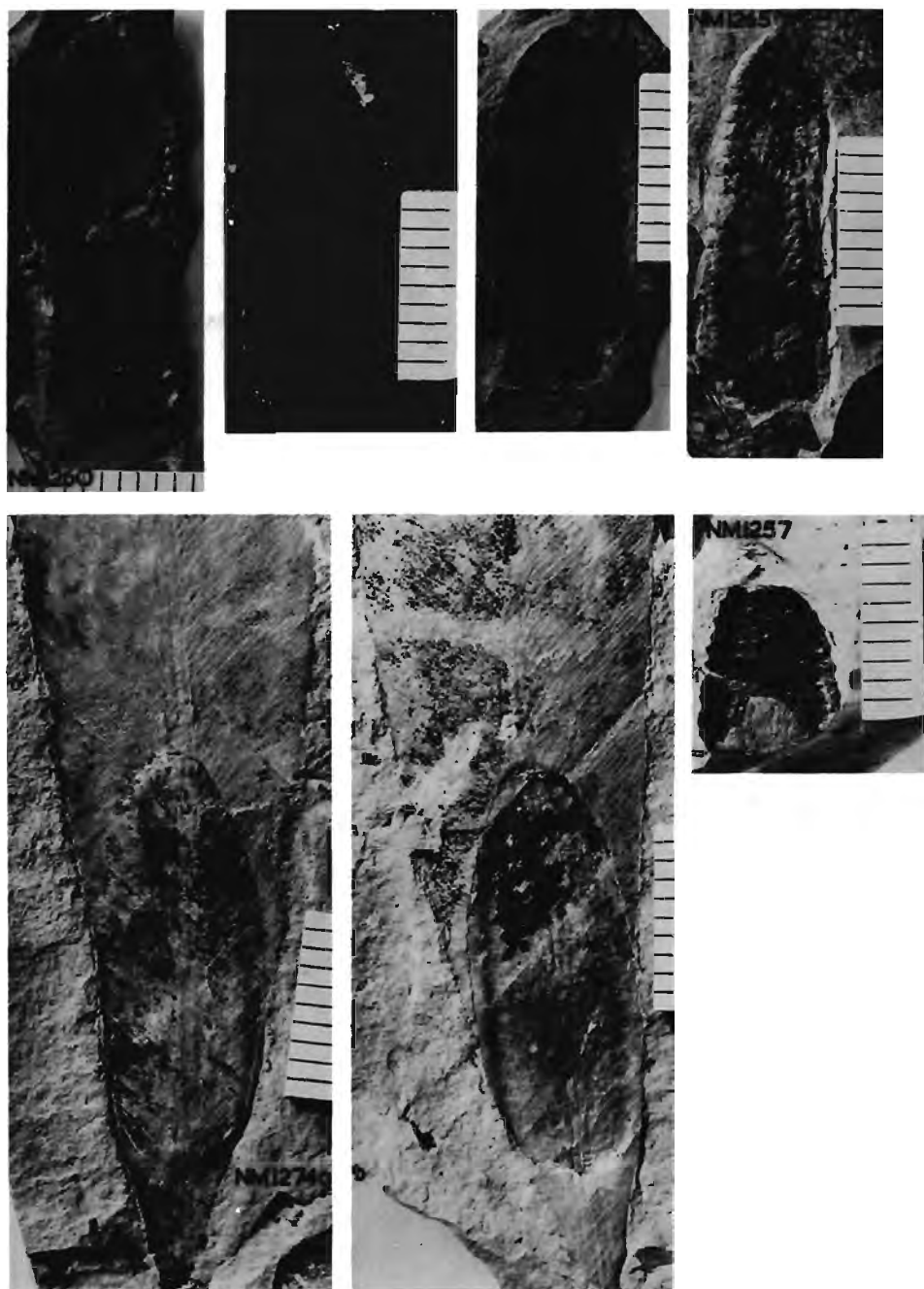
Holotype: NM 1260.

Description and discussion: The dimensions given above are derived from an examination of the fourteen most complete specimens, including those attached to leaves, but the following description takes all the specimens into account.

In the detached specimens it is usually difficult to decide whether the fructification was an originally flattened bifacial organ bearing sacs on one side only or whether it was a cylindrical organ bearing sacs over its entire surface, that is on both sides in a flattened condition after compression during fossilization. Surange & Maheshwari (1970) believe that *Scutum* falls into the latter category; and Surange & Chandra (1973a) have demonstrated clearly that *Dictyopteridium sporiferum* Feistmantel was also of the cylindrical cone-like type.

A careful examination of all the specimens of *Plumsteadia natalensis* provides evidence that it was bifacial.

Most specimens lie flat and symmetrically in the shale. These appear to have a narrow wing, about 1,5 cm wide, equally developed on both sides of the fructification and crossed by lines at regular intervals.



NM 1260, 1243a, 1243b, 1265, 1274a, 1274b, 1257: *Plumsteadia natalensis* sp. nov. $\times 2,5$.

One specimen shows a scalloped edge, but this may be a result of the line of fracture of the shale (NM 1257). However, there is no true wing. The appearance of a wing is formed by the outer sides of the contiguous marginal sacs sloping inwards. In specimens of this type (specimen NM 1260) it is noticeable that the centre is raised and that it is separated on each side from the raised margin by a depressed area. This suggests that a collapse of inner, probably fleshy, tissue, except over a central, probably vascularized, core, has resulted in the pulling in of the outer sacs and has given them sloping sides, simulating a narrow wing.

This explanation is supported by the fact that occasional specimens which have no depressed areas show no wing (NM 1265) and also by the fact that one specimen (NM 1243) lies asymmetrically in the shale, with an *apparent* wing, larger than usual and more than 2 mm wide, on *one* side and *no* apparent wing on the other side.

Considered together, these various appearances are explicable in terms of an originally bifacial structure, perhaps somewhat fleshy, bearing sacs on one side only, which has undergone varying degrees of collapse and compression during fossilization. In several specimens the sacs appear to be arranged in lines which curve upwards and outwards from the centre of the fructification to the margin, suggesting that they might be associated with an underlying spreading vascular supply.

The interpretation of the circular and polygonal scars which surmount the sac-like bodies presents the same problem that it does in other fructifications of this type. The circular scars are about 0,5 mm wide, with a smooth raised outer rim, followed by a depressed ring and a raised central boss. They are not contiguous. The polygonal scars are larger, about 1 mm wide and contiguous. They possess a striated raised outer rim, a narrow depression and a raised central boss. In these details they agree closely with the postulated stages of growth of sacs in *Scutum* species described by Plumstead (1956). It remains an open question whether these elevated bodies with scars in *Plumsteadia natalensis* represent the casts of seed-containing sacs (that is units of ovary construction) as believed by Plumstead (1952, 1956), or the casts of compressed naked ovules or seeds directly attached to the surface of the fructification, as suggested by Surange & Maheshwari (1970) for an Indian specimen attributed to *Scutum*.

Occasional specimens of *Plumsteadia natalensis* show simple scars in the form of a papilla about 0,5 mm wide. These might be the scars left after detachment of sessile seeds, much in the manner demonstrated recently by Surange & Chandra (1973a) in *Dictyopteridium sporiferum*.

The attached specimens show that the new fructification was practically sessile on the midrib of a *Glossopteris* leaf on its adaxial side near the base of the lamina (NM 1274). It is attached by a wide base with the sac-bearing face uppermost, that is adaxial. The leaves are narrow, but none is complete. They range from 6 to 10 cm long and 1,5 to 1,7 cm wide. The lateral veins leave the well-marked midrib at a steep angle and pursue a straight fairly close, parallel course to the margin, with only occasional anastomoses. The general form of the leaf is that of a narrow *Glossopteris indica* and is also similar to *G. angustifolia*.

Plumsteadia natalensis most nearly resembles *Hirsutum dutoitides* Plumstead (1958), formerly placed in the genus *Scutum* Plumstead (1952). It is similar in overall shape and construction and in being attached to the midrib of a narrow *Glossopteris* leaf of the *indica-angustifolia* type. *Hirsutum dutoitides* is much bigger, however

(4.5 cm long by 2 cm wide), and is attached by a short stiff stalk to the top of the petiole. Furthermore, Plumstead (1952, 1956, 1958) described a filament-covered male part of the fructification which has not been seen in *Plumsteadia natalensis*. Plumstead separated *Hirsutum* from *Scutum* partly on the basis of the type of pollen organs, partly in the belief that it possessed a narrow, fluted, reflexed wing. It seems quite probable, however, that the appearance of a wing-like marginal structure in *Hirsutum* can be explained in the same way as that here put forward for *Plumsteadia natalensis*.

The same considerations also suggest that the Indian fructifications referred to *Scutum* by Surange & Maheshwari (1970), especially the one illustrated in their text-fig. 10 and pl. 43, fig. 20, could also be referred to *Plumsteadia*.

Some forms of *Plumsteadia natalensis* are not easily separated from *Dictyopteridium sporiferum* Feistmantel, as revised by Surange & Chandra (1973a), and as understood by Rigby (1974, pers. comm.), except on the basis that *P. natalensis* is believed to be a flattened bifacial organ, while *Dictyopteridium* is cylindrical with seeds attached all over its surface.

Seeds

Reference under appropriate headings has already been made to seeds in organic connection with named plant organs (see *Lidgettonia africana*, *Mooia lidgettonioides* and *Rusangea elegans*). Because of their attachment, these seeds are known by the names applied to the associated organs and thus need not be otherwise identified. Various kinds of dispersed seeds are common throughout the matrix. Some of these are readily identifiable with attached seeds. It is possible that immature seeds were not readily detached from the organs that bore them either before or during fossilization, whereas mature ones were disseminated naturally before this process or readily detached during it. Because the isolated, scattered seeds may thus be more mature than attached ones, and because they are so numerous, they should provide a more representative sample of size and of structural detail within each type than do the attached seeds. Thus they are dealt with here under the alphabetical symbols A–C inclusive.

Also quite common are seeds associated with scales, either in contact with (attached to ?) wing-like scales that themselves seem to have been detached from another organ (type D seed), or lying upon (probably without connection) leaf-like scales that are either lanceolate or more or less rhomboidal in shape (types E and F seeds).

The last case seems one of secondary association, the seeds having been disseminated at maturity from the organs that developed them, to fall upon and cling to (by means of sticky or finely hairy sarcotestas ?) scale- or foliage leaves of the plant on which they were developed. Less likely, but not impossible, is the association of such dispersed seeds with leaves of neighbouring plants. It is unlikely the seeds were developed *in situ*, for, in a few cases, more than one seed type is associated with an individual scale-leaf. Usually, however, the relationship is more specific, a particular seed type being present upon scale-leaves of a particular shape, but there is no apparent pattern of arrangement of the seeds on a scale-leaf. At present, the only conclusion that may be drawn confidently from study of these 'seed-bearing' scale-leaves is that seeds and scale-leaves were probably juxtaposed on the same or neighbouring plants during life.

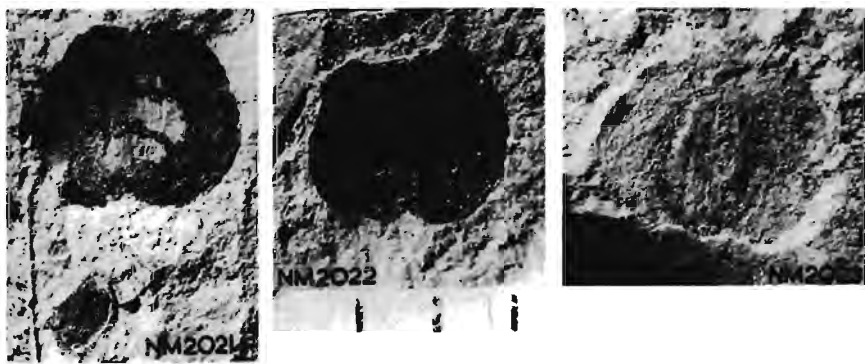
I. Dispersed seeds

(i) Winged seeds

Type A—seed of *Lidgettonia africana* (*Samaropsis* type cf. *S. seixasi* (White) Sew., 1917)

Specimens figured NM 2021, NM 2022, NM 2023

Description: Seeds platyspermic, winged, circular to slightly horizontally elliptic (wider than long), 2,0–2,5 to 3,0–3,5 mm long by 2,0–2,8 to 3,5–4,6 mm broad overall. Sclerotesta about 2 mm long by 1 mm wide, elliptic with fine longitudinal striations. Sarcotesta formed into two lateral wing-like expansions about 1 mm in width. Base almost truncate with a wide, shallow sinus; micropylar sinus well developed, broadening outwards between the rounded margins of the sarcotesta. sometimes with a short central beak (NM 1020).



NM 2021, 2022, 2023: Seeds type A (*Lidgettonia africana*) $\times 10$.

Discussion: Hamshaw Thomas (1958: 185) described isolated seeds from the type locality of *Lidgettonia africana* that agree closely both in size and form with the seeds considered above. He did not, however, find any in organic connection with cupules of this fructification as has been done with fossils from Mooi River. He went on to state (p. 187) that Seward (1917) described somewhat similar forms from a number of places under *Samaropsis*, of which *S. seixasi* (White) Sew. from Brazil resembled the Lidgetton seeds most closely. Maithy (1964: 53) stated that seeds exhibiting a range of variation in shape and structure had been placed under *Samaropsis* so that the genus had become unwieldy. He proposed a tentative scheme for further delimitation based on seed morphology. In following this scheme as a key, seeds of type A must be identified as *S. seixasi*, but no description or dimensions for the taxon are given by Maithy. However, dimensions which Thomas gives, apparently from Seward's description, are larger than present specimens (sclerotesta 8–10 mm long, 5 mm broad).

(ii) Non-winged seeds—types B and C

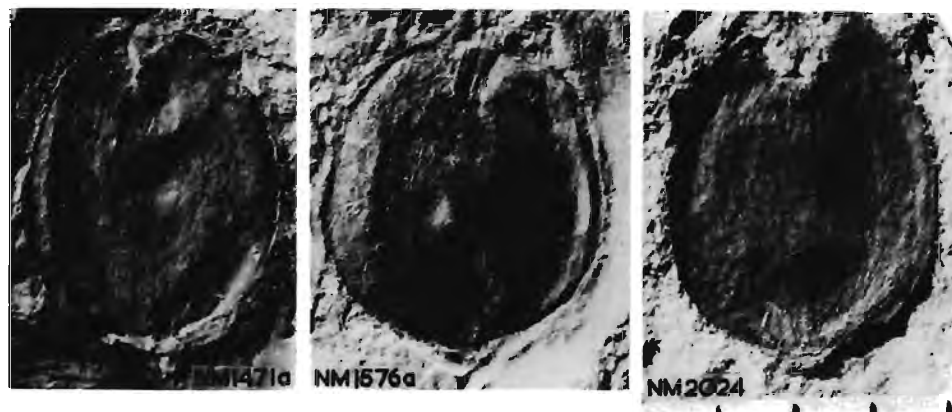
Type B—seed of *Mooia lidgettonioides* (doubtfully *Cordaicarpus* type following Maithy, 1964)

Specimens figured NM 1471a, NM 1576a, NM 2024

Description: Seeds probably platyspermic, non-winged, broadly elliptic to oblong with a poorly defined submarginal ridge or depression about 0,2 mm from periphery

(in each of several examples a ridge is present on the left-hand edge, a depression on the right, or vice versa), 2,5–3,6 to 4,0 mm long by 2,0–3,0 to 3,8 mm broad overall. Sclero- and sarcotesta not visibly differentiated. Base rounded, sinus lacking: micropylar sinus broadly V-shaped.

Discussion: Seeds of type B are clearly different from those of type A since they lack any perceptible wing and also a basal sinus. Following Maithy 1964 seeds of type B are nearest those described under the genus *Cordaicarpus*, but they do not agree well with any taxon considered by this author. This is perhaps significant since one seed of this type (NM 1471) appears to show organic connection with *Mooia lidgettonioides*, described as a new genus and species of megasporangiate fructification. Type B may thus represent a previously undescribed seed.



NM 1471a, 1576a, 2024: Seeds type B (*Mooia lidgettonioides*) $\times 10$.

Type C—probable seed of *Rusangea elegans* (generic type unknown, seed possibly of Cycadalean affinity)

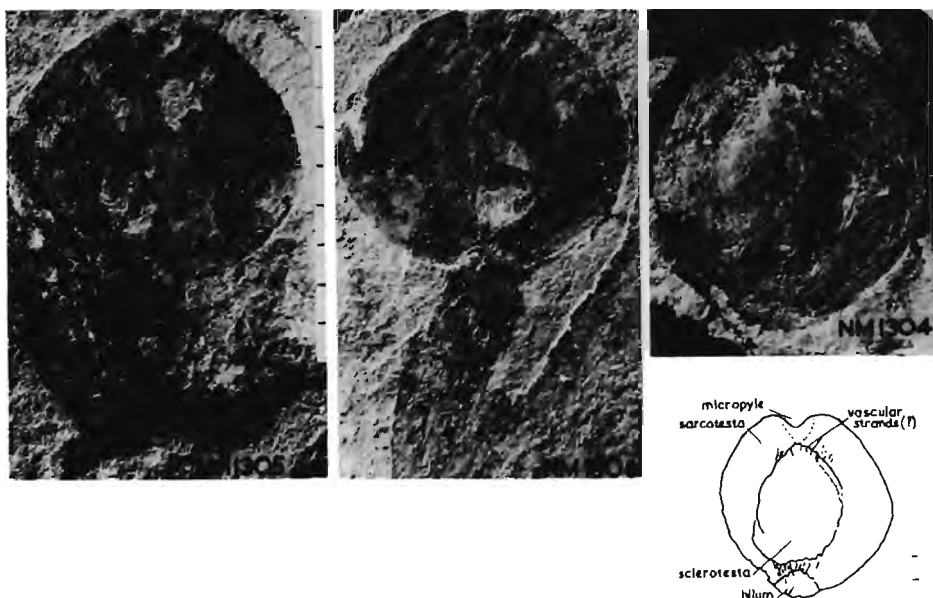
Specimens figured NM 1305, NM 1306, NM 1304

Description: Seeds possibly radiospermic, non-winged, circular (sometimes slightly longer than wide), 5,0–6,3 to 8,0 mm long by 6,0–7,3 mm broad overall. Sclerotesta about 5 mm long by 5 mm broad, circular. Sarcotesta about 2 mm wide, entirely surrounding sclerotesta except at micropylar sinus. Base rounded with a crescentic hilum scar about 2 mm in diameter: micropylar sinus broadly and shallowly funnel-shaped.

Discussion: Five isolated seeds of type C have been found. One particularly informative specimen (NM 1304) suggests the seed may have been radiospermic and fleshy. This is deduced from the following features: the sclerotesta is clearly convex suggesting compression of hard tissue: the sarcotesta is thick and appears to have been provided with numerous vascular strands, since a number of fine, ochre-coloured threads (distinct from coaly cleat markings) can be detected fanning out from the basal hilum scar and passing under the sclerotesta to emerge at its apex, where the threads are broken. It seems unlikely that a circular wing of tissue surrounding a platyspermic seed would be provided with so ample a vascular supply, if this is indeed the correct

interpretation of the fine threads. Such vascular strands are more likely to be present in the fleshy integument of a radiospermic structure.

Other specimens (NM 1305, 1306) not only repeat evidence of a broad crescentic hilum, but suggest the attachment of this to a stout, short, but incomplete, stalk which orientates the seed as orthotropous and emphasizes its massiveness. In every respect the seed seems Cycadalean. The five isolated specimens are associated with simple leaves reminiscent of those bearing attached megasporangiate structures described in this paper as the new genus and species *Rusangea elegans*. This is suggestive that type C represents seeds (possibly more nearly mature) isolated from sporophylls of this kind.



NM 1305, 1306, 1304: Seeds type C (*Rusangea elegans*) $\times 5$. (NM 1305 and 1306 are counterparts.)
 BELOW: Line tracing of seed showing crescentic hilum and lines suggestive of vascular strands.

II. Seeds associated with scales

(i) Seeds attached (?) to wing-like scales

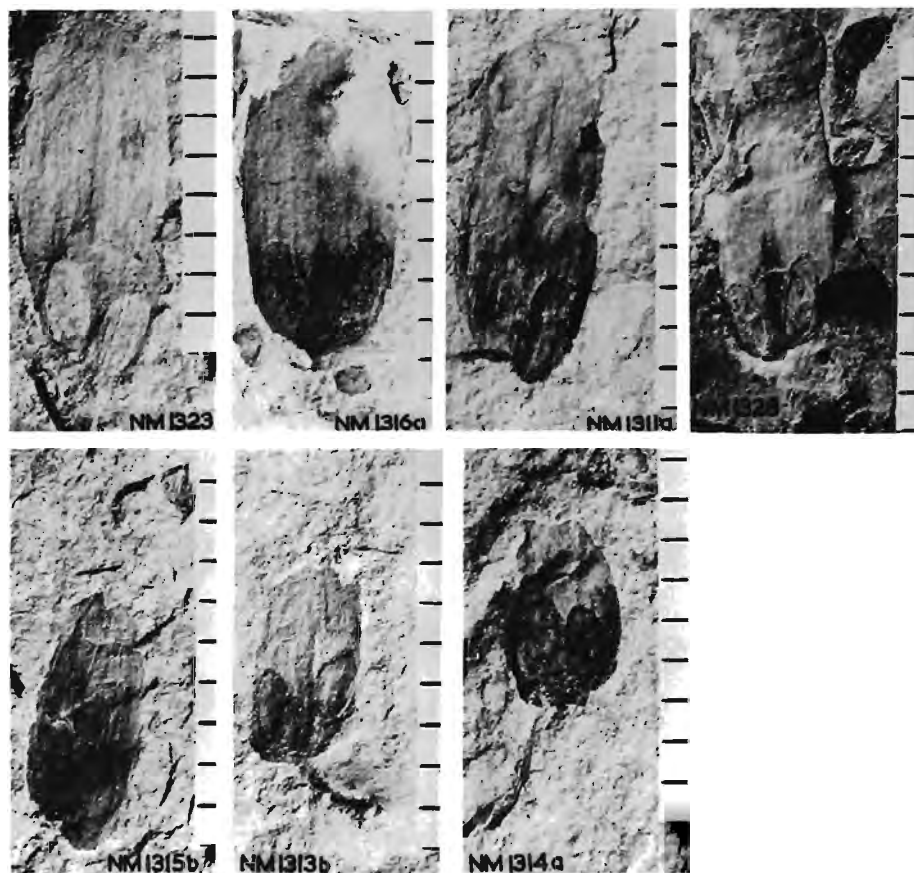
Type D

Specimens figured NM 1323, NM 1316a, NM 1311a, NM 1328, NM 1315b, NM 1313b, NM 1314a
 Description and discussion: It is not possible to describe seeds of this type formally, for their structure is not fully understood. Type D is represented by some 28 specimens. One of these (NM 1311) agrees almost perfectly in form with a text-figure of a detached ovule-bearing scale illustrated by Surange & Maheshwari (1970: 188). The size of the overall structure is also in agreement, but the seed itself is smaller in the Mooi River specimen (2,5 mm long by 1 mm wide as compared with 3,5 mm by 2 mm). Another difference is that a thin, thread-like attachment is discernible at the base of the wing near the seed, a feature apparently lacking in the Indian specimens, but present in at

least two other fossils from Mooi River (NM 1313, 1314). This may be part of the vascular supply to the seed that has pulled away from the parental organ of development as this broke up before fossilization. The text-figure of Surange & Maheshwari referred to does show, however, a slender short prolongation of the seed which may be comparable with this attachment.

Surange & Maheshwari interpreted their fossils as detached ovule-bearing scales (ovuliferous scales) and suggested 'the ovule was attached at the base of the scale, perhaps on its upper surface'. They also suggested that these ovuliferous scales ('just thin appendages, not hard woody structures as in some of the conifers') might be the reproductive units of the compact strobilus, *Scutum*, each scale-leaf bearing a single ovule.

Many of the Mooi River fossils show not one, but two seeds situated at the base of the 'scale' to left and right of centre, the one slightly above the other as the specimen lies in the matrix (NM 1313, 1315, 1316, 1323). The apex of the scale is not always smoothly truncate, but shows a shallow central sinus which suggests possibly that it is not a simple structure, but formed of two closely approximated units (perhaps two scales each carrying basally a single seed?). NM 1315 gives the best evidence for this,



NM 1323, 1361a, 1311a, 1328, 1315b, 1313b, 1341a: Seeds type D \times 5.

for there the one seed is set appreciably above the other and the 'scale tips' are equally distant. If this is the interpretation, then the frequent association of two seeds (a majority of the specimens of type D consist of two seeds only) suggests there must have been some connection between them since they have remained in association during fossilization. There is also the presence of the short 'stalk' that lies between and below the two seeds and which may serve as an attachment, but this is not evident in every case where two seeds are represented. This interpretation is not entirely satisfactory, however, as some examples show the presence of more than two seeds (three in NM 1328; four in NM 1314). It may be that the relationship of one seed to one scale as suggested by Surange & Maheshwari (1970: 190) does not meet every case, and that the scale represents a containing tube of tissue, open and poorly lobed at the distal end, in which more than one ovule may be developed proximally, that is near the point of attachment to its parental organ of development. This view is perhaps, strengthened by the faint evidence of the presence of more than one seed in pl. 43, fig. 22 of Surange & Maheshwari (loc. cit.). It also seems likely that, if one ovule developed on the surface of a scale (perhaps in the manner of *Pinus*), the outline of the ovule, in contrast to that of the thin scale, might be expected to be clearer in the fossil than often appears to be the case.

The idea of seeds developed within a tubular sheath or a cupule is not original, for Walton (1952), in reply to Plumstead's explanation of the structure of *Scutum*, suggested that the fructification was more likely to have been a strobilus or cone-like structure with a central, perhaps fleshy, axis, bearing sporangia (?) or seeds (?) each attached to a projecting lamina *that may have been tubular*.

There is at present no evidence, except that both seeds and *Scutum*-like axes occur together in the Mooi River shales, that seed type D was borne on an axis of the *Scutum* type. What does seem certain is that up to four seeds (?) or megaspores (?), usually elliptic to elliptic-oval in shape, were developed, probably within, but certainly in association with, an extension of thin, scale-like tissue possibly forming a containing tube or an enveloping sheath.

Tentative description: Seeds (?) 1-4, usually two, per 'scale', platyspermic, elliptic to elliptic-oval, 1,2-3,0 (mean 2,26) mm long, 0,6-2,0 (mean 1,04) mm wide, without markings and thus without defined chalazal and micropylar regions, except that it seems probable the chalazal end is orientated towards the apparent point of attachment to the parental unit. Associated 'scale' more or less oblong, occasionally elliptic-oblong, 4,5-10,0 (mean 7,5) mm long, 2,5-4,5 (mean 3,45) mm wide, base asymmetric, sometimes with a centrally placed, narrow, stalk-like appendage up to 3 mm long: apex more or less truncate, usually with a shallow central sinus or somewhat scalloped, occasionally rounded: surface faintly striated, but not veined.

(ii) Seeds lying upon leaf-like scales (probably without connection)

Types E and F

Specimens figured NM 1419, NM 1414a, NM 1412a, NM 1413

Twenty-six specimens of lanceolate to elliptic-lanceolate foliage or scale-leaves with seeds lying upon them (probably without direct connection) have been found. A further 27 are similar except that the leaves are more or less rhomboidal in shape

resembling, in some cases, the cupule-bearing sporophylls that are named *Lidgettonia africana*.

Study of these 50-odd examples has revealed the following facts:

1. An individual leaf appears to have the seeds associated with only one surface: this is even the case where a lanceolate leaf has been folded at right angles across the midrib (NM 1412). In two specimens only (NM 1459, 1442) is there the possibility that seeds were lying upon both leaf surfaces. In NM 1459 one seed is clearly defined on the exposed leaf surface; the outline of a second seed is visible 'under' leaf tissue suggesting this second seed could have been lying upon the undersurface of the leaf. It could, however, also have been lying in the matrix under the leaf when fossilization occurred. NM 1442 shows the impression of a seed on the exposed surface; a second seed of the same type is visible at a lower level, the matrix having eroded and thus exposed it. Neither specimen is entirely convincing as an example of a leaf with seeds lying on both surfaces.

2. It is always difficult to be certain whether ad- or abaxial leaf surfaces are exposed when the shale splits. In some cases with the seed-bearing scales under consideration a conclusive decision was impossible, but for the majority, venation and curvature of the leaf, especially towards the petiole base, provided sufficient evidence to suggest that in 18 specimens seeds lay on the adaxial leaf surface, while in 29 specimens seeds lay on the abaxial surface. Thus seeds were found associated with *both* leaf surfaces, but in each individual specimen the seeds were *either* adaxial *or* abaxial.

There were only two exceptions to this.

3. There is no particular pattern of orientation of the seeds on the leaves. In specimens where many seeds are present (NM 1412, 1415) some lie with micropylar ends directed to the leaf apex, others are reversed, while in others the micropylar axis lies at right angles to the midrib. Some seeds lie entirely on the leaf surface, others are marginal overlapping into the surrounding matrix. Where a leaf has been folded at right angles to the midrib (NM 1412), one seed appears to extend from the leaf tissues into the matrix at this point as though it had lifted from the leaf surface at folding. The seeds do not always lie isolated from one another: in many cases, especially where the seeds are crowded, there is partial overlap of one with another.

4. The seeds associated with individual leaves are usually, but not always, of only one type.

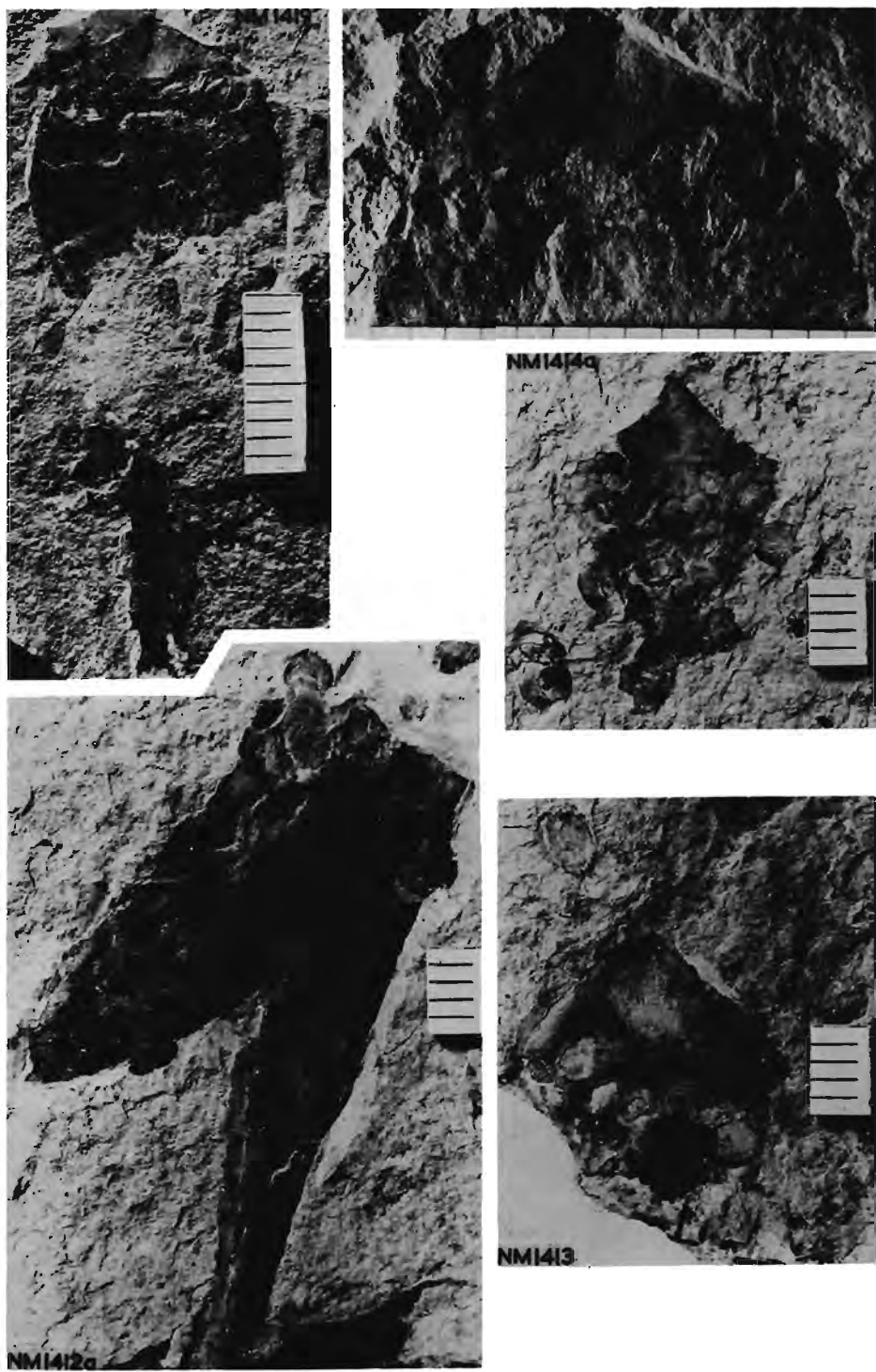
5. When more than one type of seed is represented on a leaf, usually the majority are of one type, few being of a second type.

6. Not more than two seed types have been found associated with any individual leaf.

7. These seed types are:

a. *Type E*. This type is by far the most common. Many leaves carry 1–4 such seeds. Fewer leaves carry more seeds, the numbers 6, 7, 8, 10, 15, ± 22 and ± 28 all being represented. Where many seeds are present, these are seldom uniform in size, but vary indiscriminately from small to larger.

Tentative description: Seeds possibly platyspermic (? since they lie on the leaf surface), non-winged, circular to slightly horizontally elliptic in outline, 2.2–4.0 mm long, 2.0–4.5 mm wide overall. Sclerotesta about 2 mm long by 2.5 mm wide, often with fine longitudinal markings. Sarcotesta surrounding sclerotesta, about 1 mm



NM 1419 and 1419 enlarged, 1414a, 1421a, 1413: Seeds type E and type F $\times 2,5$.

wide. Base broadly rounded without a sinus: micropylar sinus, if present, not clearly defined.

In dimensions and in the striated sclerotesta these seeds are comparable with those of seed type A, attributed to *Lidgettonia africana*, but they differ in not being winged and in the absence of comparable chalazal and micropylar sinuses. They do not resemble seed type B in either dimensions or structure. Structurally they are like seed type C, but are considerably smaller and there is little evidence of the broad crescentic hilum scar. In view of these differences, the seeds usually found lying upon (?) leaves must be considered of a type distinct from others so far described in this paper.

b. *Type F*. Seeds of this type are not numerous. In some cases (for example NM 1412 — two type F seeds) a few occur scattered among seeds of type E. They resemble seed type B in structure, but the V-shaped micropylar sinus is lacking and they are smaller. Information is too scant to attempt formal description.

Discussion: It is considered significant that in the Mooi River shales leaves with seeds directly associated with them, especially in large numbers, are small in size suggesting they are scale-leaves or sporophylls rather than true foliage leaves. Few large *Glossopteris* leaves, which are by far the commonest plant remains in the fossil beds, have been found with associated seeds. Where this has occurred, it must be considered a chance relationship. The scale-leaves which carry three or more seeds (of which there are about 40 examples) cannot be considered the outcome of chance association, especially as isolated seeds of the same type (or any type for that matter) are not frequent in the ambient matrix. Some scale-leaves bearing only solitary seeds have been included in the present account, but the seeds were always of seed type E, and seemed to form part of the scale-seed association under consideration. There are others that have been excluded, however. These are scale-leaves (sporophylls ?) that have, in every case, only solitary seeds associated with them. The seeds resemble type E, but are considerably larger suggesting seed type C, which in turn was likened previously to the megasporangium of *Rusangea elegans*. Such specimens are few, and in almost every case the seed is marginal, partially overlapping into the surrounding matrix. It is suspected that such specimens may be sporophylls of the *Rusangea* type, each with a solitary megasporangium associated without visible evidence of connection. Thus they should rather be considered under *Rusangea elegans* than in the context of scale-leaves with seeds lying upon them.

CONIFEROPSIDA

CORDAITALES OR CONIFERALES

Genus *Noeggerathiopsis* Feistmantel, 1879

Noeggerathiopsis hislopii (Bunbury) Feistmantel

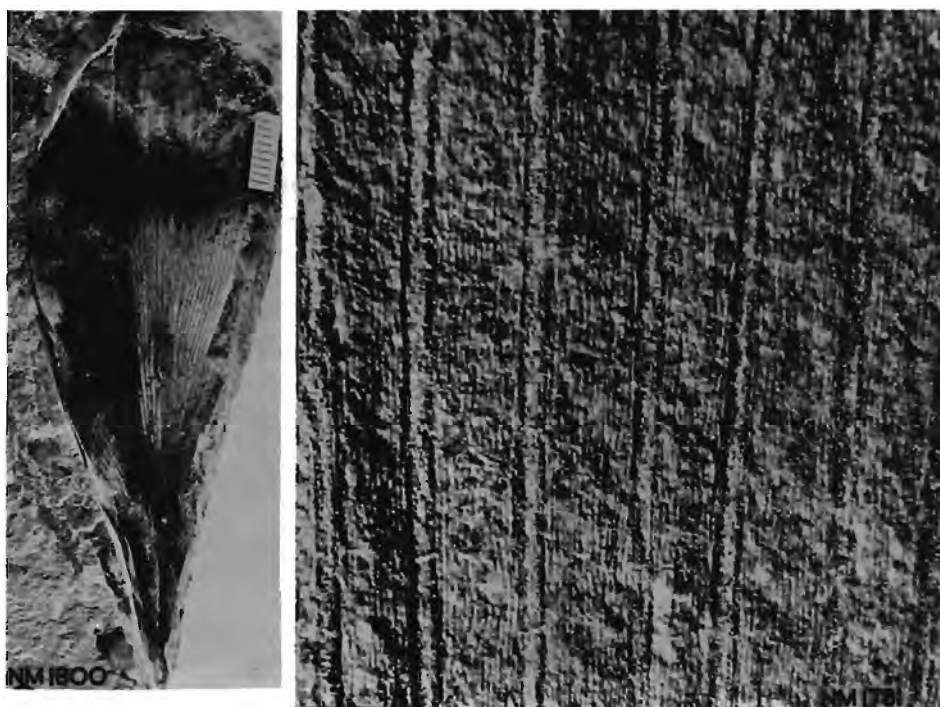
Specimens figured NM 1800, NM 1781

The collection contains 23 specimens of this distinctive leaf. Many are fragmentary, lacking base or apex, but all show the rather coarse, almost parallel, occasionally forking veins which are characteristic of the species. Complete leaves are slightly asymmetrically obovate, widening gradually from a very narrow base to attain maximum width about one-third of the distance from the round or bluntly pointed apex.

The best-preserved complete leaf (NM 1800) is 7,5 cm long and 3 cm wide, with a base only 1,5 mm wide, but the occurrence of fragmentary leaves over 3,5 cm across their widest part shows that considerably larger sizes were attained.

Some of the leaves show a cellular pattern (NM 1781), but no cuticles are preserved.

Particular interest centres on the shape and small size of the leaf base and on the number of veins in that region. An examination of four intact bases shows an adaxially canaliculate structure, ranging from 1,0 to 2,5 mm wide, and probably with four veins. These features suggest that these *Noeggerathiopsis* leaves could have been borne on slender twigs (see later under *Incertae Sedis*) which have spirally arranged rhomboidal to crescentic scars, each with two vascular imprints. The reduction from the four veins seen in the leaf bases to two vascular scars on the twigs could have been achieved by fusion of bundles in the cortex; a similar arrangement is known, for example, in the Northern Hemisphere Palaeozoic genus *Cordaite*s and also in extant *Ginkgo* and *Araucaria*.



NM 1800, 1781 enlarged: *Noeggerathiopsis hislop*ii (Bunbury) Feistmantel $\times 1$ and $\times 20$.

*Noeggerathiopsis hislop*ii has usually been regarded as a cordaitan leaf on the grounds of a general macroscopic similarity to species of *Cordaite*s. It should be noted, however, that, according to Lele & Maithy (1963), the epidermal structures of *Cordaite*s and *Noeggerathiopsis* are not closely related. Furthermore, the reproductive structures of *Noeggerathiopsis* are not known. The classification of *Noeggerathiopsis* is therefore problematical. While a cordaitan affinity is probable, reference to the Coniferales is not excluded.

INCERTAE SEDIS

Rigbya arberioides gen. et sp. nov.

Specimens figured NM 1644a and b, NM 1646a, NM 1669a, NM 1650, NM 1656

Thirty-one specimens of this problematical fructification have been obtained. They consist of an aggregation of seed-bearing scales, or possibly cupules, borne in a fan-shaped arrangement on a long slender stalk. There are no indications that they belong to the Glossopteridaceae, though this is possible.

They differ from previously described reproductive structures in Lower Gondwana floras and the new name *Rigbya arberioides* is proposed for them. The genus is named for John F. Rigby in recognition of his extensive contributions to the palaeobotany of various parts of Gondwanaland and for his assistance in the preparation of the present account.

The specific name refers to the similarity between the Mooi River plants and *Arberia minasica* (White) emend. Rigby (1972a).

Combined diagnosis: Female fructification consisting of a stalk bearing a terminal flabellate aggregation of seed-bearing scales.

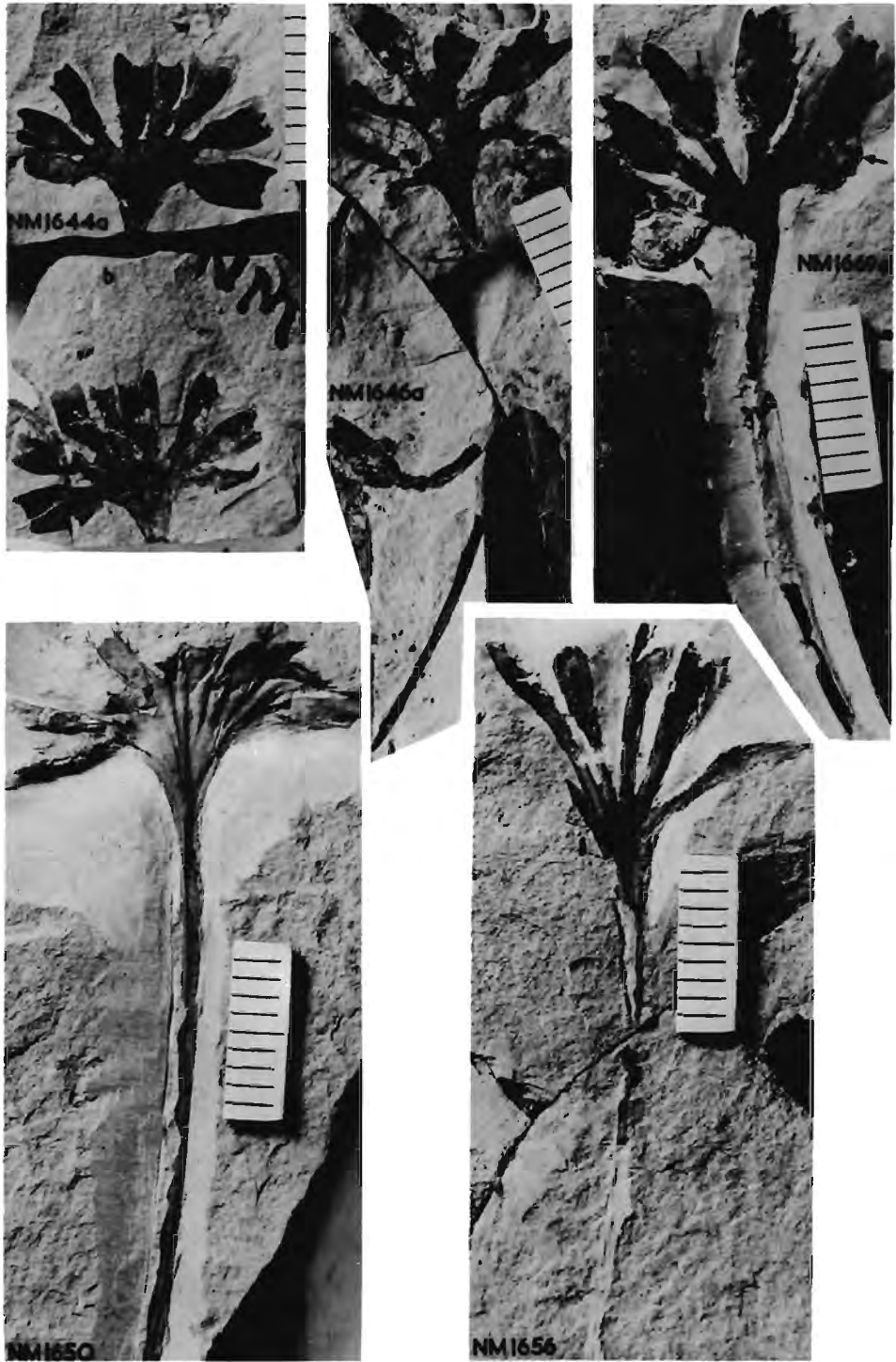
Stalk, its branches and terminal scales all longitudinally striated. Stalk slender, canaliculate, about 0,5 to 1,0 mm wide, slightly expanded at the base, usually straight, occasionally slightly curved, attaining at least 5 cm in length, expanded at the distal end up to about 4 mm, then dividing repeatedly, with close dichotomies, to form a dorsiventral flabellate cluster of five to ten, most frequently six, distal scales.

Scales 0,5 to 1,3 cm, most frequently 0,8 cm long, 2 to 3 mm wide, expanding from a narrow base to become elongate-spathulate and usually terminating in two pointed lobes.

Scales convex, swollen at right angles to the flattened plane of the fructification, each enveloping one seed at its base (perhaps representing a one-seeded cupule). Seeds 3,0 to 3,5 mm long and 2,5 to 3,0 mm wide, ovoid, flattened, but not winged, Holotype: NM 1669.

Description: The numerous specimens of *Rigbya arberioides* show a wide range in size and form. In some of the larger examples (NM 1650) the terminal branching is condensed and long scales are apparently fused laterally, giving the whole structure a fan-like appearance.

In other specimens (NM 1656) the terminal system is not much branched, but the scales are long and quite free from one another. In most specimens (NM 1644, 1646) the scales are shorter and clearly borne on a branching system. These forms are regarded as all belonging to one species, because all have the same longitudinally striated surface and the same swollen lobed form of the terminal scales. Moreover, the range of variation is continuous. Three specimens unequivocally bear seeds. One particularly instructive specimen (NM 1669) has six terminal scales with evidence of a seed in five of them. The *position* of the seed is sometimes indicated by a swollen area at the base of the terminal scale, just above its narrow stalk. In other instances the large flattened seed has been exposed in this position by *dissecting away* the upper surface of the scale. It is not quite certain whether the terminal scale was a flattened structure which bore the seed on one side near its base or whether it was a channelled or tubular structure which enveloped the seed and hence formed a one-seeded cupule. The similarity to the one-seeded cupules of the Northern Hemisphere Coal-Measure



NM 1644a and b, 1646a, 1669a, 1650, 1656: *Rigbya arberioides* gen. et sp. nov. $\times 2,5$.

Pteridosperms *Lagenospermum* and *Gnetopsis* is quite striking. *Rigbya arberioides* is regarded as a female *Pteridosperm* fructification.

Discussion: *Rigbya arberioides* has much in common with *Arberia minasica* White, as revised by Rigby (1972a). The similarity extends to (1) the repeatedly forking terminal branch system, (2) the ultimate segments bearing seeds, (3) the ornament of longitudinal striations.

The two fructification types differ in that *Arberia minasica* (1) bears very numerous branches scattered along its rachis and not aggregated into a distinct head or capitulum, and (2) its seeds were borne on the recurved tips of the branchlets and not some way down the terminal segments. If Rigby (1972a) is correct in stating that *Arberia minasica* has no evidence of cupules and if it should prove that the terminal scales of *Rigbya arberioides* are at least partially surrounding the seeds and hence cupulate, then it will not be possible to include this Mooi River fructification in Rigby's (1972a) new Family *Arberiaceae*, despite the close similarities.

Rigbya arberioides shows close similarities also with the fructification from Antarctica described by Schopf (1967) as a dorsiventrally flattened, unisexual, possibly ovulate, capitulum of *Glossopterid* affinities.

Rigby (1972a) discusses Schopf's Antarctic fructification and compares it with a single pinna of a specimen resembling *Arberia* from New South Wales, Australia (Rigby 1972a: pl. 26, figs 5, 6 and 7 and text-fig. 3D). More recently, Rigby (1974, pers. comm.) has provided a latex pull of a further fructification of Upper Permian age from the Upper Bowen Series at Burngrove Creek, Queensland (No. GSQ F4642). This specimen has a slender stalk about 1 mm thick and 2,5 cm long, which expands into a flattened head composed of several, possibly seed-bearing, scales each about 5 mm long and 2 mm wide. It is suggested that the Antarctic fructification and the fructifications from New South Wales and Queensland in Australia should all be included in *Rigbya arberioides*.

In the case of *Arberia*, Rigby (1972a) points out that there is little resemblance to 'the better-known attached *Glossopteris* fructifications such as *Scutum*, *Lanceolatus* and *Ottokaria*'. Much the same might be said for *Rigbya*, although it is possible to see slight similarity between the latter and *Ottokaria* since both are dorsiventrally flattened fructifications borne on long slender stalks.

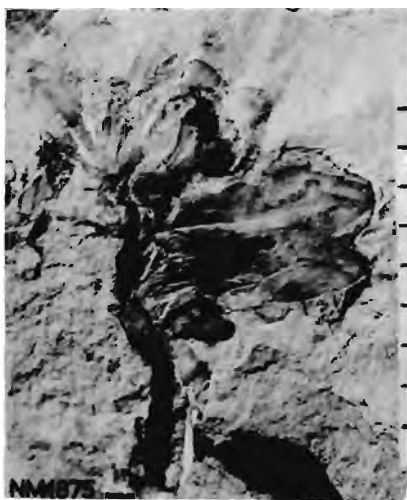
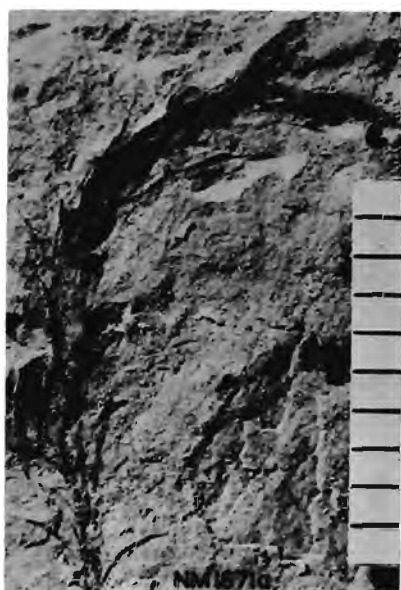
***Buthelezia mooiensis* gen. et sp. nov.**

Specimens figured NM 1880b, NM 1871a, NM 1872a, NM 1875

Among the specimens from Mooi River are ten very small leafy shoots which, while defying satisfactory classification, are nevertheless well characterized. Furthermore, they are of some interest in that they bear rhizoids or root-hairs and may represent complete plants.

Accordingly, the new name *Buthelezia mooiensis* gen. et sp. nov. is proposed for them. The genus is named for Chief Buthelezi of KwaZulu in recognition of his interest in conservation and the importance of the fossiliferous areas of KwaZulu, and the species *mooiensis* is named for the district of Natal in which the plant occurs. Combined diagnosis: Small leafy shoots. probably complete plants, at least 17 mm long. Stems ranging from 0,5 mm to about 1,5 mm in diameter, bearing spirally

arranged leaves. Leaves about 3,5 to 7,0 mm long, 0,5 to 2,0 mm wide, entire, flat throughout their length. Smaller leaves lanceolate and nearly parallel-sided, larger leaves ovate-lanceolate, all acutely pointed, traversed by a single strong median vein, more prominent on the lower side, persistent to the apex, where it ends in a sharp, almost hair-like, point. Leaves attached to the stem by a broad sheathing base, ascending steeply for a short distance, then spreading at a wide angle, occasionally reflexed.



NM 1880b, 1871a, 1872a, 1875: *Buthelezia mooiensis* gen. et sp. nov. $\times 5$.
INSET: Line tracing of plant showing stem, attached leaves and basal rhizoids (?).

Rhizoids or root-hairs arising in tufts at the lower end of the stem. Fructification unknown.

Holotype: NM 1880.

Discussion: *Buthelezia mooiensis* cannot be classified with certainty at present. Comparisons with several groups of the Plant Kingdom are possible.

The small size of the plant, the apparently delicate nature of its leaves with sheathing bases and the presence of tufts of rhizoid-like appendages on the lower part of the stem strongly suggest bryophytic affinities. General comparison is possible with some of the Permian mosses described by Neuburg (1956, 1958, 1960) from Angarida, U.S.S.R. It should be noted also that plants strikingly similar to extant species of *Dicranum* Hedw. have been described by Plumstead (1966) from the Upper Carboniferous of several localities in the Transvaal, while Townrow (1959) has described a moss resembling extant species of the Leucodontaceae from the Molteno (Middle Triassic) of the Umkomaas valley in Natal.

However, the facts that the stems often bear a fair amount of residual carbonaceous matter and that the mid-vein of the leaf is very prominent, coupled with the possibility that the basal tufted structures might be root-hairs, suggest an alternative explanation. These small leafy specimens could be juvenile stages of a lycopod sporophyte. In this connection, it should be noted that there is very close agreement in almost all respects with the description of small leafy shoots of the lycopod *Cyclodendron leslii* (Seward) Kräusel from Uganda given by Du Toit (1932b). The chief difference is one of size, the leaves of the specimens described by Du Toit being about five times larger than in the Natal material.

An affinity with coniferalean shoots, while not impossible, seems unlikely in view of the delicate nature of the plant, its leaves and rooting structures.

On balance, the evidence is perhaps just in favour of regarding *Buthelezia mooiensis* as a moss, probably colonizing the mud-flats in the area of deposition of the rich Mooi River Flora.

Axes with leaf cushions

Specimens figured NM 1726, NM 1723

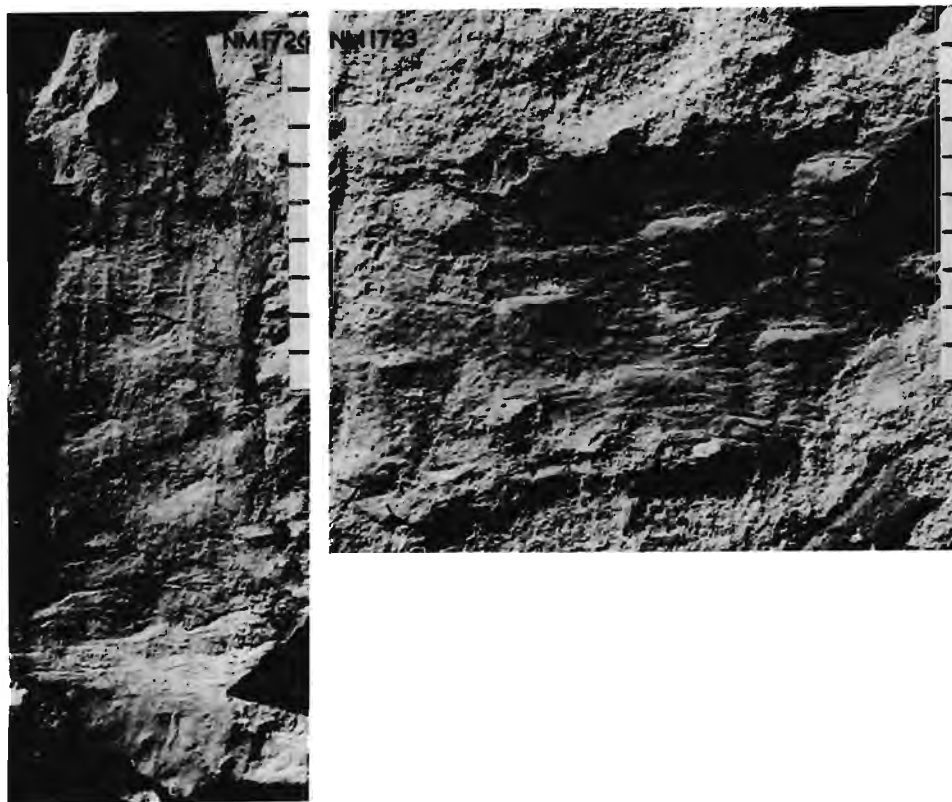
Twelve very small fragments of axes bearing spirally arranged leaf cushions have been found. Most of them appear to be pieces of bark. In general the leaf cushions have a transversely extended rhomboidal shape. They vary from about 1 to 3 mm wide and from about 0,3 to 1,5 mm deep. They may be contiguous or widely separated. In the latter case the stem surface between the leaf cushions is ornamented with transverse wrinkles or striations. One specimen (NM 1726) is particularly informative. It is not a fragment of bark, but part of a twig, about 0,7 cm wide and 1,7 cm long. It bears rhomboidal cushions like the other specimens, but there is a clear indication of zones of contiguous and of separated cushions occurring in the same specimen. The contiguous cushions are about 3 mm wide and 1,5 mm deep, while the separated cushions are smaller, about 2 mm wide by 1 mm deep, with the ornament of transverse wrinkles between them.

The leaf cushions themselves have certain distal features. In seven of the twelve specimens this takes the form of two small circular scars, placed side by side transversely. These scars are about 0,15 mm wide and 0,5 to 0,75 mm apart. They appear

as raised papillae on some cushions and as depressions in others. In the depressed condition the circular scars are often occupied by residual carbon. In two specimens, including one photographed (NM 1726), it is difficult to decide whether or not there is a third, less-conspicuous mark between the two circular scars. In the remaining three specimens markings on the leaf cushions are obscure.

It has not proved possible to identify these leaf-cushion-bearing fragments. They resemble small branches of the lycopsid *Cyclodendron leslii* (Seward) Kräusel (Kräusel 1928) very closely, especially in the transversely rhomboidal leaf cushions and the occurrence of zones of crowded cushions (interpreted by Plumstead (1969) as indicating seasonal growth). But the presence of *two* scars on the leaf cushion distinguishes the present specimens from *Cyclodendron leslii*, which is said to have only a single central vascular scar. Even if it were possible to regard the two scars in the Mooi River material as two parichnos scars lateral to an obscure vascular scar, Gondwana lycopsids are excluded, since Kräusel (1961) states categorically that no parichnos scars are present in *Cyclodendron* Kräusel and the related genera *Lycopodiopsis* Renault and *Lycopodiaphloios* Kräusel, all of which occur in South Africa.

If the twin scars in the present specimens are regarded as indicating two vascular bundles in the leaf cushion, an alternative attribution is possible, namely that these



NM 1726, 1723: Axes with leaf cushions $\times 5$.

fragments are part of coniferalean twigs. They might well have borne the leaves of *Noeggerathiopsis hislopii* Feistmantel, which are fairly common in the same beds. As pointed out earlier (p. 408), the *Noeggerathiopsis* leaves have a transversely extended base, only about 1,0 to 2,5 mm wide, and the vascular supply in this region is reduced certainly to four, possibly to fewer, strands.

The occurrence of zones of contiguous cushions alternating with zones of dispersed cushions, and the presence of a surface ornament of transverse wrinkles, are not distinguishing features. They are known to occur in both Lycopsida and Coniferophyta.

DISCUSSION

Composition of the Mooi River Flora

The following is a list of the various taxa recorded up to the present:

Sphenopsida

Phyllothea australis Brongniart

P. cf. etheridgei Arber

cf. Raniganjia bengalensis (Feistmantel) Rigby

Sphenophyllum speciosum (Royle) McClelland

Pteropsida

Sphenopteris alata (Brongniart) Brongniart

Cycadopsida

Glossopteris browniana Brongniart

G. indica Schimper

G. angustifolia Brongniart

G. cf. leptoneura Bunbury

G. feistmantelii Rigby

G. conspicua Feistmantel

G. cf. ampla Dana

G. elongata Dana

Belemnopteris elongata sp. nov.

Glossopterid scale leaves (various)

Eretmonia natalensis Du Toit

Arberiella sp. (detached microsporangia)

Lidgettonia africana Thomas

Mooia lidgettonioides gen. et sp. nov.

Rusangea elegans gen. et sp. nov.

Scutum conspicuum comb. nov.

Plumsteadia natalensis sp. nov.

Dispersed winged seeds (type A)

Dispersed non-winged seeds (types B and C)

Seeds attached to wing-like scales (type D)

Seeds associated with linear and rhomboidal leaf-like scales (types E and F)

Coniferopsida

Noeggerathiopsis hislopii (Bunbury) Feistmantel

Incertae Sedis

Rigbya arberioides gen. et sp. nov.

Buthlezeria mooiensis gen. et sp. nov.

Axes with leaf cushions
and additionally (to be described in a later paper)
bisaccate pollen grains
slender leafy twigs
Dictyopteridium sp.

Botanical considerations

The flora is characterized by an abundance of sphenopsid, pteropsid, cycadopsid and coniferopsid leaves, fructifications of eight different kinds, dispersed seeds and microsporangia. Bryopsids and lycopsids have not been recognized with certainty. Even if *Butholezia mooiensis* should later prove to be a lycopsid, such plants would constitute a very minor element in the flora. The lycopsid *Cyclodendron leslii* (Seward, Kräusel, known elsewhere in South Africa (Du Toit 1954), has not been found.

No so-called 'northern' elements, such as occur in the Wankie Flora (Lacey & Huard-Moine 1966), have been recognized.

The fructifications present a number of problems. In the first place, seven distinct kinds of seed-bearing (or probably seed-bearing) organs have been found (*Lidgettonia africana*, *Mooia lidgettonioides*, *Rusangea elegans*, *Scutum conspicuum*, *Plumsteadia natalensis*, *Rigbya arberioides*, *Dictyopteridium* sp.), but only one kind of microsporangiate organ (*Eretmonia natalensis*). Does this mean that male organs show much less variation and that one basic type serves for fertilization of the different seed-bearing organs, all of which probably belong to the Glossopteridales? Or are there several types of male organ, differing only slightly from one another, included in *Eretmonia natalensis* as understood in this paper?

A second question concerns the manner in which the various fructifications, male and female, were borne by the parent plants. Several examples have been found of sterile scales and of microsporangium-bearing scales of *Eretmonia* type occurring associated in groups. While associated sterile scales could simply be a group of bud-scales, they could equally well be a group of sterile scales from the base or apex of a strobilus, such as commonly occurs in many extant conifers. Associated microsporangium-bearing scales strongly suggest that the male organs were aggregated together on a branch. Considering these points together with the fact that many of the fructifications described earlier show great variation in shape, size and length of the basal portion, it seems reasonable to suggest that at least some of them were borne in lax strobili. This applies particularly to *Eretmonia natalensis*, *Lidgettonia africana*, *Mooia lidgettonioides* and *Rusangea elegans*.

Scutum conspicuum and *Plumsteadia natalensis* are known to be borne on *Glossopteris* leaves. It may well be that these leaves, together with their reproductive structures, were also borne in clusters on short shoots or in loose strobili. *Rigbya arberioides* and the as yet undescribed *Dictyopteridium* are detached organs and their attribution is problematical.

Thirdly, the fructification of *Noeggerathiopsis hislopii* is still unknown. This plant is generally referred to the Cordaitales, but no seed-bearing organs remotely resembling the Northern Hemisphere genus *Cordaianthus* have been found in Gondwanaland.

Finally, it must be pointed out that all the dispersed seeds have been grouped together under Cycadopsida in this account for convenience in description. It may be

that the dispersed seed of *Noeggerathiopsis hislopil*, from an as yet unknown fructification, is included here.

The problem of chance and real association of fossil plant organs is always difficult. It is hoped that a statistical analysis of the specimens available in the as yet unworked large reserve slabs of shale will provide information on the association of one kind of organ with another at the Mooi River site. This work will also form the basis of a later paper.

Geological considerations

(a) Age of the Mooi River Flora

According to Du Toit (1954) species of the genus *Gangamopteris* McCoy do not extend beyond the Ecca in South Africa, while *Glossopteris elongata* Dana (syn. *G. retifera* Feistmantel) extends through the Ecca and Lower Beaufort. Since more than one thousand specimens have been examined from the Mooi River locality and no examples of *Gangamopteris* found, it can be accepted that this genus is not present.

The absence of *Gangamopteris*, considered in conjunction with the presence of *Glossopteris elongata*, therefore indicates a Lower Beaufort (Upper Permian) age for the Mooi River beds.

This dating is also supported by the occurrence of *Glossopteris conspicua* Feistmantel, a species which Du Toit (1954) regarded as characteristic of Lower Beaufort and higher horizons.

Plumstead (1972) has suggested that *Phyllothea etheridgei* Arber and *Dictyopteridium sporiferum* Feistmantel may also indicate a Lower Beaufort (Upper Permian) age.

The associated insect fauna (Riek 1973) also indicates an Upper Permian age.

The Mooi River floral assemblage falls within the *Daptocephalus* reptile zone, but knowledge of Lower Beaufort floras has not yet reached the point where zonation by plants and by animals can be properly equated. It may well be that, with further field-work, the fructification genera *Eretmonia*, *Lidgettonia*, *Mooia*, *Rusangea* and *Rigbya* will prove to be useful stratigraphical index fossils within the Lower Beaufort of Africa.

(b) Comparison with other parts of Gondwanaland

India

The Mooi River Flora compares closely with that of the Raniganj Stage (Upper Damuda Series) in India. Taxa described in this paper which support this comparison and correlation are:

Phyllothea australis Brongniart

P. cf. etheridgei Arber

cf. Raniganjia bengalensis (Feistmantel) Rigby

Glossopteris feistmantelii Rigby

G. conspicua Feistmantel

G. elongata Dana

Belemnopteris elongata sp. nov.

Eretmonia natalensis sp. nov.

Seeds attached to wing-like scales (type D)

Australia

Comparison with the Upper Permian Newcastle Series of New South Wales and Upper Bowen Series of Queensland is suggested by the following taxa:

Phyllothea australis Brongniart

P. cf. etheridgei Arber

Sphenopteris alata (Brongniart) Brongniart

Glossopteris feistmantelii Rigby

G. conspicua Feistmantel

Rigbya arberioides gen. et sp. nov.

Dictyopteridium sp.

Antarctica

The occurrence of *Belemnopteris elongata* sp. nov. in Natal and at Terrace Ridge, Ohio Range (Schopf 1970) and of *Rigbya arberioides* gen. et sp. nov. in Natal and at Mercer Ridge, Ohio Range (Schopf 1967) suggests an Upper Permian age for these two Antarctic localities and horizons.

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